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The Taxonomy, Host Range and Geographic Distribution of the Genus Pythium

By

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THE TAXONOMY, HOST RANGE AND GEOGRAPHIC DISTRIBUTION OF THE GENUS PYTHIUM

JOHN T. MIDDLETON

INTRODUCTION

This investigation was prompted by the need for a study of the genus *Pythium* which would contribute toward a better understanding of the species, their taxonomic status, and their phylogeny.

The genus has been treated systematically at least five times since its establishment in 1858. Several distinctly different dispositions have been made. New species from various hosts from widely scattered areas throughout the world have been described. A review of the literature concerning the species indicates some of them to be synonymous, others of doubtful validity and still others imperfectly delineated. Since 1931–1932, when the last account of the genus was published, a comparatively large number of species have been described but not given any taxonomic treatment. In the following discussion an attempt is made to assemble information from many scattered papers and indicate the salient parts. New data resulting from observation, research and analysis are presented and already existing data are amplified and evaluated.

An effort was made to secure from various hosts and localities as many cultures as were available of the described species as it was assumed that a study of a group of isolates would be more representative than the study of a single isolate and would enable the investigator to determine the extent and nature of variation within a natural system. The majority of the cultures employed in this study were supplied by various individuals interested in the genus. Wherever possible the host and locality from which the fungus was obtained are given. Cultures listed as being from Baarn are from the Centraalbureau voor Schimmelcultures, Baarn, Holland.

Keys for the identification of the species were often found to be inadequate, emphasis frequently being placed upon the host infected or the growth habit of the fungus when grown on certain culture media. The need for a classification of the species became more apparent as the work progressed. A natural system of classification based upon the morphology of the species seemed most desirable; a key utilizing the principles of this system is therefore supplied.

To further aid students of the genus and plant pathologists encountering members of the genus as plant pathogens, information relative to host and geographic distribution is included. In addition to a summary and condensation of the available literature on this phase of the work, the extent and variety of hosts have been materially amplified. This information is appended to the discussion of the individual species and cross-indexed for the reader's convenience.

MORPHOLOGICAL OBSERVATIONS

Mycelium

The mycelium of *Pythium* is made up of rather fine filaments, measuring from 1 to 8 μ, usually 2 to 5 μ, in diameter. The filaments are cylindrical, usually irregularly branched, hyaline and coenocytic when young. As the thallus matures, septa are laid down in a random fashion, serving to separate the empty portions of the hyphae, formed by the apically directed protoplasmic movement, from the full ones. The hyphae may be either intramatrical or extramatrical, usually both when grown on solid substrates. When a multicellular host is invaded the hyphae develop both intercellularly and intracellularly.

The method by which the hyphae penetrate the cell wall is not clear. Appressoria are usually formed when the hyphae make a surface contact. Appressoria may be simple or complex, straight, curved or globular in shape, becoming more or less flattened when applied to a firm surface. They may be discerned readily because of their dense protoplasmic contents. Though at times confused with certain filamentous sporangial types, they may be distinguished from these by their failure to develop zoospores. Although appressoria are found in both filamentous and spherical sporangial types, they seem to be most abundant and most readily produced in the former.

Sporangia

Sporangial germination in *Pythium*, as previously indicated, is characterized by the passage of the protoplasm in an undifferentiated state through a short or long emission tube into an evanescent apical vesicle in which the zoospores are formed. This process takes place in ten to fifty, and usually in fifteen to twenty, minutes. Sometimes the term sporangium is used in place of the term vesicle as used here; the structure from which the vesicle arises in turn is called pre- or prosporangium. The writer concurs with the opinion given by Fitzpatrick (1930) that this terminology only leads to confusion, particularly in *Phytophthora* where no vesicle is produced and the structure gives rise to zoospores directly.

There are two principal types of sporangia in the genus *Pythium*, filamentous and spheroidal. The occurrence of these two distinctly different types of sporangia provides a convenient basis for separation of the species.

The filamentous sporangia may be indistinguishable from the vegetative thallus or somewhat inflated. When strictly filamentous, they may be simple or branched, acrogenous or intercalary, but in any case cut off from the supporting hypha by a septum. They usually may be recognized by their rather dense protoplasmic content. The sporangia of *Pythium gracile*, *P. dictyosporum*, and *P. monospermum* are good examples of the strictly filamentous type.

Pythium aphanidermatum, *P. arrhenomanes*, *P. graminicolum*, and *P. torulosum* exemplify the inflated filamentous type of sporangia, usually more

or less complex in structure, consisting of several communicating dactyloid or lobulate elements which extend outward in all directions. The individual lobes vary from 8 to 20 μ in diameter and are densely filled with protoplasm. The sporangia of *P. periilum* and *P. myriotylum*, though typically inflated filamentous, are more or less intermediate in form between *P. monospermum* and *P. arrhenomanes*. The sporangia of *P. periilum* are composed of sparingly distributed swollen digitate elements which may or may not be arranged in complex units; they also have entirely undifferentiated vegetative elements. *P. myriotylum* is much like *P. periilum* with regard to its sporangia except that the inflated lobulate elements are more numerous.

The spheroidal sporangia vary considerably in size, shape, and position on the supporting hyphae. The range in size in a single species may be as much as 30 μ. This is well illustrated in *Pythium debaryanum* in which the measurement of 200 sporangia gave a range of from 8.1 to 39.4 μ in diameter. (Measurements taken of 200 sporangia of each species studied are omitted here as including them would not contribute to the usefulness of this study.) The sporangia are usually spherical to elliptical in shape in most species, as exemplified in *P. debaryanum*, *P. spinosum* and *P. ultimum*. Frequently, however, they are spherical to subspherical, ovate to obovate, pyriform and truncate. All these sporangial shapes may be found in a single species, as exemplified by *P. irregulare*.

A sporangium unique in the genus is exhibited in *Pythium anandrum*, *P. helicoides*, *P. oedochilum*, *P. palingenes*, and *P. polytylum*. These species possess sporangia which are usually spherical to obovate and possess a sessile apical papilla.

Several species, including *Pythium megalacanthum* and *P. proliferum*, possess proliferous sporangia. Proliferation manifests itself in two ways: the secondary sporangium is formed within the previously emptied sporangium; the supporting hypha of the secondary sporangium grows up through the primary sporangium to form the secondary structure outside and above the primary one.

The sporangia of the spheroidal type may be acrogenous, intercalary, or laterally sessile. When they are acrogenous, the sporangiophore may vary in length from 5 to 400 μ, no definite length being associated with a particular species. Intercalary sporangia are usually single but may be grouped. Grouped sporangia fall into two classes: in one the sporangia are of individually spherical parts contiguous to similar structures by means of an undifferentiated filament; in the other they are spherical and separated from the supporting hyphae by septa but connected serially to form a catenulate structure. *Pythium acanthicum* and *P. oligandrum* are examples of the former and *P. intermedium* typifies the latter.

When properly treated, the sporangia germinate in a characteristic and peculiar manner. The sporangium, whether filamentous or spheroidal, gives rise to a delicate emission tube which is usually from 2 to 5 μ in diameter and

which varies from 5 to 500 μ in length. The protoplasm of the sporangium flows into an evanescent vesicle; here cleavage of the protoplasm takes place to produce the zoospores. In rare instances the protoplasm may be discharged from the vesicle in an undifferentiated state, collecting at the periphery of the vesicle and delineating the zoospores exogenously. In no instance are zoospores formed within the sporangium.

The sporangia of all filamentous strains invariably germinate by the production of zoospores. Though the sporangia of spheroidal strains usually produce zoospores they frequently germinate by the production of one to six germ tubes. These spheroidal structures which germinate by germ tubes have been occasionally referred to as conidia. It is true that asexual reproductive bodies which do not give rise to spores cannot correctly be termed sporangia. Conidia are, however, commonly considered to be deciduous and are borne on stalks which are morphologically distinguishable from the mycelium from which they arise, except perhaps the micronemal conidia of Saccardo. No spheroidal asexual reproductive bodies in this genus are considered truly deciduous nor are they borne on supporting hyphae that are distinguishable morphologically from the mycelium. The use of the word deciduous is qualified here, for in species producing catenulate reproductive bodies those at the apex are frequently dislodged, not akin to falling off at maturity, the basal series remaining in position; it is contended that this is not truly a deciduous condition, especially as no new structure is produced in its place subsequent to its removal. Further, these reproductive organs may germinate either by the production of zoospores or of germ tubes depending on environmental factors. The one exception is *Pythium ultimum* in which species zoospore formation is unknown. In view of these facts it seems desirable to designate the asexual reproductive structures in this group of species as sporangia rather than as pseudosporangia, pseudoconidia or conidia, inasmuch as morphologically and phylogenetically only one structure is under consideration.

Zoospores

The zoospores are reniform, possessing two lateral cilia which arise from a hilum located on the concave side. The number of zoospores produced in a vesicle varies from two to 125, possibly more. Information pertinent to the cytology of zoospore formation in *Pythium* is lacking; a detailed cytological study of a similar process occurring in *Plasmopara halstedii* (Farlow) Berl. and de Toni is given by Nishimura (1926). After an active stage in which the zoospores move rapidly about in water, they encyst and assume a spherical form varying from 4 to 18 μ, mostly from 8 to 12 μ, in diameter. Zoospores are monoplanetic and ordinarily germinate by the formation of a germ tube. Repeated emergence has been observed rarely in species possessing large zoospores, the spores sending out an evacuation tube from 2 to 3 μ wide and from 5 to 30 μ long, capped by a vesicle in which usually a single, though rarely from two to six zoospores are formed. A single zoospore of some species

may undergo as many as six repeated emergences. These escape from the vesicle, encyst, and then germinate by a germ tube. This process has been erroneously referred to as diplanetism. Since only one type of swarmspore is produced a true diplanetic condition does not exist; rather, typical spore germination merely recurs; this phenomenon is termed repetitional emergence or secondary spore formation.

Cornu (1872) is apparently the first to observe repetitional emergence in his study of *Pythium proliferum* in which he observes the production of secondary zoospores. Butler (1907) portrays this behavior in his consideration of *P. diacarpum*, referring to it as diplanetism. Atkinson (1909) corrects Butler's interpretation, calling it secondary spore formation rather than diplanetism. Drechsler (1930b) also mistakenly refers to the repeated emergence of zoospores of *P. butleri* and *Phytophthora* spp. as diplanetism.

Oogonia

Oogonia exhibit less variation in shape than sporangia; they are usually spherical to subspherical when acrogenous and elliptical to limoniform when intercalary, and always delimited from the supporting hyphae by a septum. Oogonia vary from 6 to 75 μ in diameter. The measurement of 200 oogonia of each species studied showed that though each species had a certain range and mean size, the ranges and means were so very similar, overlapping and often identical, that no taxonomic value could be assigned to them; these data are therefore omitted.

Structures resembling oogonia, if not identical with them, have been observed to produce germ tubes under suitable conditions, which again emphasizes the fact that the oogonium is a vegetative structure and that it may also serve as an asexual reproductive body. This has been demonstrated in *Pythium ultimum* by the writer (Tompkins *et al.* 1939).

The wall of the oogonium is thin, about 1 μ thick, and may have either a smooth or an echinulate surface. The echinulations are merely extensions of the oogonial wall and may or may not be cut off from the oogonium by septa. The spines may be short or long, conical or curved, with sharp or blunt apices, or may be digitate, mammiform, or papillate.

The spines of *Pythium irregulare*, *P. mamillatum*, and *P. megalacanthum* are often proliferous, becoming much elongated. A single spine in *P. mamillatum* formed an oogonium at its tip which was fecundated by a monoclinous antheridium to produce an apparently normal oospore. Instances of this sort are exceptional.

The smooth or echinulate character of the oogonial wall and the type of echinulation are specific characters. Utilization of these characteristics is made in the classification of the species.

At maturity the protoplasm of the oogonium differentiates into two not very clearly defined regions, the central region becoming the oosphere and the peripheral region the periplasm. It is the oosphere that becomes the

oospore upon fertilization, the periplasm either contributing to the oospore wall or degenerating and not becoming a part of the oospore.

Antheridia

Soon after the oogonial initial is formed the antheridia generally become discernible. They may vary in size, shape, number, and place of origin. An antheridium may be allantoid, clavate, globose, suborbicular, or trumpet-shaped, borne terminally or intercalarly. The antheridial stalk is as often short as long and is frequently absent. The number of antheridia per oogonium varies from none to twenty-five and possibly more, though usually numbering between one and four.

There are three types of antheridia, based on their point of origin; they are hypogynal, monoclinous, and diclinous. Any of these may make only apical contact with the oogonium or may apply its entire length, in any case producing a short, narrow fertilization tube that penetrates the oogonial wall and permits the passage of the antheridial gonoplasm into the oogonium.

A hypogynous antheridium is one surmounted by an oogonium; the antheridium is formed either within the oogonial stalk or at the apex of the oogonial stalk adjacent to the oogonium, never laterally disposed. A monoclinous antheridium originates at any site along the oogonial stalk, while a diclinous antheridium arises from any hypha of the same thallus other than the oogonial branch.

The term "androgynous" is often employed in the discussion of the point of origin of antheridia in this and related genera. "Androgynous" does not accurately describe the antheridial habit because it means only that the antheridia and oogonia occur together and does not explain the way in which the antheridia and oogonia are really associated. The use of the words "androgynous" and "diclinous" as antinyms does not seem justified and it appears advisable to supplant "androgynous" with "monoclinous."

The origin and morphology of the antheridium is a specific characteristic and is considered a valuable criterion for specific identification.

Oospores

A single oospore is regularly formed in an oogonium, though occasionally two and even three have been observed. The oospores vary from 4 to 48 μ in diameter and are spherical with a smooth or reticulate wall which may be either thin (0.6 to 1.8 μ thick) or inspissate (1.8 to 3.8 μ thick). Oospores which fill the oogonial cavity are termed plerotic, while those that do not fill it are called aplerotic.

The oospore is filled with rather opaque, granular protoplasm usually containing a single reserve globule and a single refringent body. However, four species, *Pythium helicoides*, *P. oedochilum*, *P. polytylum*, and *P. palingenes*, constitute an exception, having several (from 5 to 30) reserve globules and several (from 2 to 8) refringent bodies.

Oospore germination is not commonly observed and is unknown in some species. Germination may be accomplished either by the production of one or several germ tubes or by the formation of zoospores. Oospore germination is most commonly seen in *Pythium acanthicum* and *P. vexans*.

The plerotic or aplerotic condition of the oospore and the thickness and type of the oospore wall are characters which are sufficiently stable to permit their use in the morphological segregation of the species of this genus.

Homothallism

The genus *Pythium* seems to be consistently homothallic. Sparrow (1931b) indicates that *Pythium adhaerens*, though possessing diclinous antheridia, is homothallic. Vanterpool (1939) reports that this is the case in *P. arrhenomanes*, *P. butleri* (= *P. aphanidermatum*), *P. myriotylum*, *P. torulosum*, and *P. complectens* (= *P. vexans*). More recently Wen-chun Ho (Ho *et al.* 1941) demonstrated that *P. graminicolum* is homothallic. The writer substantiates these observations and presents additional instances of homothallism.

In order to determine whether or not certain species were homothallic, isolates were cultured from individual hyphal tips and single zoospores. The fungus was first grown in Petri dishes on corn meal agar, a small block of agar containing the fungus was then removed and plated out on plain water agar. From two to four days later a piece of agar was removed containing an individual hyphal tip; this in turn was plated out on a substrate favorable for sexual reproduction. In single zoospore cultures, the fungus on water agar plates was allowed to develop until sporangia were produced. Subsequently either a fairly large agar block was removed and placed under irrigation in a glass vessel or the entire plate was irrigated (a glass vessel was tilted so that slowly running tap water completely covered the agar block and flowed freely over the surface); either technique was equally successful. Immediately following zoospore production the excess liquid was withdrawn and a few milliliters of liquid containing actively swimming zoospores were drawn into a pipette and removed to another Petri dish of plain water agar. Here the zoospores were singled out and allowed to germinate; subsequent to germination they were transferred to a substrate appropriate for sexual reproduction. This technique was repeated a number of times for several different isolates of a single species.

Whenever an isolate capable of reproducing sexually was used, cultures arising both from single hyphal tips and individual zoospores produced the sexual stage. Furthermore, the sexual stage exhibited through these two techniques was identical with that of the original isolate in all respects, emphasizing the stability and utility of the type and position of the oogonium and type, disposition and origin of the antheridium, if any, in specific identification.

Species which have been demonstrated by the author to be homothallic by both techniques are: *Pythium acanthicum*, *P. anandrum*, *P. aphaniderma-*

tum, *P. aristosporum*, *P. arrhenomanes*, *P. debaryanum*, *P. dissotocum*, *P. graminicolum*, *P. helicoides*, *P. indigoferae*, *P. irregulare*, *P. mamillatum*, *P. monospermum*, *P. myriotylum*, *P. oedochilum*, *P. oligandrum*, *P. paroecandrum*, *P. periilum*, *P. periplocum*, *P. perniciosum*, *P. polymastum*, *P. rostratum*, *P. salpingophorum*, *P. spinosum*, *P. tardicrescens*, *P. torulosum*, *P. vexans*, and *P. volutum*.

Employing the hyphal tip procedure outlined, *Pythium ultimum* was found to be homothallic. Inasmuch as zoospores are not produced in this species it was impossible to determine whether similar results would have been obtained had this method been used.

Two isolates tentatively assigned to *Pythium arrhenomanes* which have failed to produce the sexual phase on all media so far tried were used in making single zoospore cultures. The sexual apparatus failed to appear in the numerous zoospore cultures made.

Zoospores produced as the result of oospore germination in *Pythium acanthicum* were also used in making single zoospore cultures. The results obtained were identical with those secured from employing zoospores from sporangia.

Most species of *Pythium* exhibit antheridia which would usually be considered as typical of a homothallic fungus. The few species displaying antheridia generally thought unique to a heterothallic fungus are in reality those of a homothallic one. *P. arrhenomanes* has been thought heterothallic by some because of the frequent failure of the species to produce the sexual stage, this failure being associated with the absence of compatible sexual strains. The results cited above demonstrate that the failure to produce the sexual stage is due to some factor other than a heterothallic condition.

GROWTH AND REPRODUCTION

The fungi were grown on several kinds of culture media so that information on mycelial growth and production of reproductive organs might be obtained. The media used were potato-dextrose agar (100 g. potato tuber, 20 g. dextrose, 15 g. agar, 1 l. water), oatmeal agar (60 g. ground oatmeal, 10 g. agar, 1 l. water), lima bean agar (60 g. ground lima bean, 15 g. agar, 1 l. water), corn meal agar (50 g. yellow corn meal, 15 g. agar, 1 l. water), plain water agar (15 g. agar, 1 l. water), and pea broth (crushed canned peas steeped in water for twelve hours).

Stock cultures of the fungi were maintained on potato-dextrose agar slants, stored at 25° C. All cultures grew satisfactorily at this temperature.

All species grew on the media used. The maximum aerial mycelial development occurred on potato-dextrose agar, the growth habit of the fungi being best exhibited on this substrate. Limited aerial growth was produced on the oatmeal, lima bean, and corn meal agars, while little if any aerial development occurred on water agar and pea broth.

Several growth habits may be recognized when the fungi are cultivated on

potato-dextrose agar. These may be described as arachnoid, cumulous, pulvinate, radiate, and rosette. Some species have both pulvinate and arachnoid and intermediate habits of growth, which makes distinction between these types sometimes difficult if not impossible. The species may be arranged in groups according to growth habit. No species may be identified accurately solely on its macroscopic growth characteristics, for the various strains of a single species vary and species morphologically dissimilar may have identical growth habits. The amount of aerial mycelium varies with the strains used. The arachnoid and pulvinate groups contain the largest number of species, the rosette, radiate, and cumulous groups containing fewer.

The arachnoid habit of growth is common to *Pythium afertile*, *P. anandrum*, *P. aphanidermatum*, *P. arrhenomanes*, *P. artotrogus*, *P. debaryanum*, *P. graminicolum*, *P. helicoides*, *P. myriotylum*, *P. nagaii*, *P. oedochilum*, *P. oligandrum*, *P. paroecandrum*, *P. perniciosum*, *P. salpingophorum*, *P. spinosum*, and *P. ultimum*.

The pulvinate habit of growth is exhibited by *Pythium acanthophoron*, *P. aristosporum*, *P. megalacanthum*, *P. monospermum*, *P. periilum*, *P. plerosporon*, *P. polymastum*, *P. polymorphon*, *P. pulchrum*, *P. scleroteichum*, *P. splendens*, *P. tardicrescens*, and *P. volutum*.

The rosette habit of growth is well displayed by *Pythium deliense*, *P. diameson*, *P. indigoferae*, *P. mamillatum*, *P. rostratum*, *P. torulosum*, and *P. vexans*.

Only three species exhibit the radiate habit of growth; they are: *Pythium hypogynum*, *P. torulosum*, and *P. vexans*.

Cumulous growth is common to *Pythium acanthicum* and *P. periplocum*.

Asexual and sexual reproductive organs are usually produced within from three to eighteen days when the fungi are grown on potato-dextrose, oatmeal, lima bean, corn meal, and water agars; only rarely were sexual organs produced in pea broth. Corn meal and water agar proved to be the most satisfactory media for studying sexual reproduction. Very little difficulty was encountered in inducing production of sexual organs in the majority of species. Oogonia, antheridia, and oospores are formed more frequently intramatrically than extramatrically. The oospores of *Pythium arrhenomanes*, *P. graminicolum*, and *P. scleroteichum* frequently were aborted if the pH of the media was above 6.0. Oospores of these species were more perfectly formed on corn meal agar than on any other substrate. In the event oospores fail to form on corn meal agar the addition of humus extract (Rands and Dopp 1933) may assist in their production. Johann (1928) devised a grated carrot agar which facilitates the formation of oospores in species renitent to produce them in standard media. If neither of the above remedies alleviate the condition media preparations including whole or macerated portions of the host plant from which the fungus was obtained may be employed. Frequently the addition of a small amount of soil rectifies the situation.

The production of asexual reproductive bodies was most abundant when the fungi were grown in pea broth for five days, the mycelial weft then being washed and placed in a continually irrigated container. Similar, though generally not as satisfactory, results were obtained when corn meal, lima bean, and oatmeal agar blocks containing the mycelium of the fungus were subjected to irrigation. Continual irrigation seems to be necessary for zoospore formation in most species, though a few produce them in limited numbers without continuous watering. This is probably true because of the necessity of removing staling products produced by the fungi and for the maintenance of an adequate oxygen supply, both of which functions this process accomplishes. Species in which it is difficult to induce production or germination of asexual reproductive bodies often yield when lima bean agar blocks containing the fungus are suitably irrigated; the process may be hastened by the addition of a small amount of soil or decaying organic matter.

No differences that could be used as an aid to specific segregation were found in the numbers and types of reproductive organs produced on the various agars.

TEMPERATURE-GROWTH RELATIONS

The effect of temperature upon the mycelial development of various *Pythium* spp. in the writer's collection was determined.[1]

Isolations of the species were grown on corn meal agar prepared from a concentrate produced by the Digestive Ferments Company, Detroit, Michigan. Glass culture tubes, 2.1 by 20.0 cm., were used. They were provided with a dam at the open end, made by heating the glass and indenting one side. These culture tubes were originally described and used by Tompkins and Gardner (1935). About 13 ml. of corn meal agar, pH 6.0, was added to each tube and allowed to cool at a uniform depth with the tube in a horizontal position, the dam preventing the escape of the melted agar.

The tubes containing the medium were inoculated near the dam at the open end with small squares of potato-dextrose agar containing the mycelium of the fungus cut from two-day-old Petri dish cultures. Inoculated tubes were left at room temperature for twenty-four hours, the extent of growth at the close of that period being indicated by a wax pencil mark on the tube; subsequent measurements were made from this point. Two tubes of each culture were placed in a horizontal position in controlled temperature chambers ranging from 1° to 46° C. at 3° intervals.

The cultures were incubated for a 72-hour period. The average growth of the fungi, in millimeters, over 24-hour periods at the various temperatures is presented in table 1.

[1] Grateful appreciation is expressed to Professor M. W. Gardner, Division of Plant Pathology, University of California, for the facilities afforded for this phase of the work.

TABLE 1. Mycelial growth of *Pythium* spp. on Difco corn meal agar at various temperatures.*

Organism	Average growth in millimeters over 24-hour period at															
	1° C.	4° C.	7° C.	10° C.	13° C.	16° C.	19° C.	22° C.	25° C.	28° C.	31° C.	34° C.	37° C.	40° C.	43° C.	46° C.
P. acanthicum	0	0	0	3	5	7	10	12	15	18	18	14	7	4	0	0
P. acanthophoron	0	0	0	0	1	2	5	7	9	7	3	2	t	0	0	0
P. afertile	1	3	7	8	10	13	17	19	21	22	23	20	11	t	0	0
P. allantocladon	0	0	3	5	7	10	13	15	16	17	18	6	0	0	0	0
P. anandrum	1	3	8	10	13	15	18	20	21	22	10	t	0	0	0	0
P. aphanidermatum	0	0	0	6	11	16	24	29	34	41	49	51	47	44	5	t
P. aphanidermatum var. *hawaiiensis*	0	0	0	3	6	9	14	17	20	22	29	31	30	26	4	1
P. araiosporon	1	3	5	7	10	12	16	20	22	24	26	22	6	0	0	0
P. aristosporum	0	t	3	6	9	12	15	17	19	20	19	7	t	0	0	0
P. arrhenomanes	0	t	2	6	9	12	18	20	22	25	22	19	7	3	0	0
P. arrhenomanes var. *canadensis*	0	t	3	5	7	10	15	19	20	23	21	15	2	0	0	0
P. arrhenomanes var. *hawaiiensis*	0	0	3	6	9	12	16	19	22	25	28	22	3	0	0	0
P. arrhenomanes var. *philippinensis*	0	t	2	4	7	10	13	15	18	22	23	22	2	0	0	0
P. artotrogus	t	4	8	11	14	19	25	31	34	36	26	5	t	0	0	0
P. artotrogus var. *macracanthum*	t	5	7	11	15	19	24	27	30	34	30	6	0	0	0	0
P. ascophallon	0	0	1	2	3	5	10	13	15	18	18	10	0	0	0	0
P. butleri	0	0	0	3	6	10	20	26	31	36	38	41	38	37	6	1
P. complectens	0	0	t	2	3	5	10	13	16	17	16	13	0	0	0	0
P. complens	0	1	2	4	5	6	8	10	11	12	13	11	2	0	0	0
P. debaryanum	1	4	7	11	15	18	24	28	30	32	28	14	1	0	0	0
P. debaryanum var. *pelargonii*	t	3	7	11	15	18	23	27	30	33	34	23	1	0	0	0
P. deliense	0	0	0	2	5	10	18	23	26	31	34	35	28	27	t	0
P. diameson	0	0	4	7	9	11	13	15	16	15	7	t	0	0	0	0
P. dissotocum	1	3	5	7	9	10	12	15	16	17	16	8	0	0	0	0
P. echinulatum (cf. *P. acanthicum*)	0	0	2	4	6	8	12	15	17	19	20	18	11	3	0	0
P. epiphanosporon	0	t	1	3	6	8	13	16	18	15	10	8	1	0	0	0
P. euhyhyphon	0	t	2	4	6	8	10	12	14	16	17	9	1	0	0	0
P. fabae	1	2	6	9	13	16	20	23	25	23	17	4	t	0	0	0
P. graminicolum	0	t	3	7	10	12	17	20	23	27	22	16	2	0	0	0
P. helicoides	0	0	0	t	2	6	18	23	28	33	36	38	35	15	2	0
P. hyphalosticton	0	t	2	4	7	10	15	19	21	24	24	19	6	0	0	0
P. hypogynum	1	2	3	4	5	6	7	9	11	13	15	16	1	t	0	0
P. indigoferae	0	0	0	t	1	3	6	9	10	11	12	9	t	0	0	0
P. intermedium	1	4	7	9	12	16	19	21	23	24	19	2	0	0	0	0

t = trace.

* Additional confirmatory data can be supplied upon request.

TABLE 1—(*Continued*)

Organism	Average growth in millimeters over 24-hour period at															
	1° C.	4° C.	7° C.	10° C.	13° C.	16° C.	19° C.	22° C.	25° C.	28° C.	31° C.	34° C.	37° C.	40° C.	43° C.	46° C.
P. irregulare	0	t	4	8	13	18	22	27	32	36	30	14	2	0	0	0
P. leiohyphon	0	0	t	4	6	8	12	15	18	15	12	6	t	0	0	0
P. leucosticton	0	0	1	3	5	7	10	12	14	16	16	12	t	0	0	0
P. mamillatum	2	3	7	11	14	17	21	24	25	26	23	13	0	0	0	0
P. mastophorum	0	0	t	3	5	7	10	11	12	7	1	0	0	0	0	0
P. megalacanthum	0	t	1	2	3	5	7	9	7	3	t	0	0	0	0	0
P. monospermum	0	2	3	5	8	10	12	14	16	18	20	17	1	0	0	0
P. myriotylum	0	0	0	t	5	9	18	21	25	30	37	42	43	40	1	0
P. nagaii	0	t	1	3	5	7	10	11	12	14	15	8	1	0	0	0
P. oedochilum	0	0	0	3	6	9	15	18	21	23	20	16	1	t	0	0
P. oligandrum	0	0	0	5	9	13	17	23	25	28	30	23	7	t	0	0
P. oryzae	1	3	5	7	9	11	14	16	18	20	16	10	0	0	0	0
P. paroecandrum	0	0	2	10	14	18	21	24	29	28	24	5	1	0	0	0
P. periilum	0	0	3	7	11	14	20	24	27	30	33	27	2	t	0	0
P. periplocum	0	0	0	t	6	14	23	27	31	34	35	32	22	1	0	0
P. perniciosum	0	3	5	7	9	10	12	14	16	18	19	15	4	0	0	0
P. piperinum	0	0	t	1	3	5	8	12	14	16	17	14	t	0	0	0
P. plerosporon	1	3	5	7	9	11	14	17	18	21	23	11	3	t	0	0
P. polyandron	0	0	2	5	8	10	14	18	20	23	25	19	4	0	0	0
P. polycladon	0	0	t	2	5	8	12	15	17	18	12	4	0	0	0	0
P. polycladon var. *chamaihyphon*	0	0	t	2	5	7	10	14	18	20	20	6	0	0	0	0
P. polymastum	0	3	6	8	10	12	14	16	18	20	19	18	7	0	0	0
P. polymorphon	t	4	7	10	12	14	18	20	21	22	17	12	0	0	0	0
P. pulchrum	0	1	4	7	9	11	14	16	18	13	10	1	0	0	0	0
P. rhizophthoron	0	0	2	5	8	11	17	21	24	27	28	12	1	0	0	0
P. rostratum	0	1	2	3	4	5	6	7	8	6	4	t	0	0	0	0
P. salpingophorum	0	1	6	10	15	19	24	28	31	33	33	11	t	0	0	0
P. scleroteichum	0	0	0	2	5	8	16	21	24	21	8	0	0	0	0	0
P. spaniogamon	0	t	2	4	9	12	17	21	26	27	23	12	5	0	0	0
P. spinosum	0	2	6	11	17	20	28	32	33	33	26	9	3	0	0	0
P. splendens	0	1	3	5	7	10	13	15	17	21	21	13	0	0	0	0
P. splendens var. *hawaiianum*	0	0	t	6	8	13	23	28	34	36	35	14	0	0	0	0
P. tardicrescens	0	t	1	3	4	5	7	8	9	4	t	0	0	0	0	0
P. teratosporon	0	t	1	3	5	6	7	8	9	9	7	5	1	0	0	0
P. thysanohyphalon	0	t	2	4	6	8	10	12	14	16	17	11	t	0	0	0
P. torulosum	0	t	2	3	5	7	9	12	13	14	12	11	0	0	0	0
P. ultimum	1	5	7	11	15	17	24	28	30	34	33	17	1	0	0	0
P. vexans	0	t	2	3	5	7	9	12	13	15	14	9	0	0	0	0
P. volutum	t	1	3	4	5	6	8	9	10	8	1	0	0	0	0	0

Very little variation is noticeable in the conspecific isolates at different temperatures; this is in distinct contrast to the rather wide variation noticeable in congeneric isolates at different temperatures. Tucker (1931) reports similar observations in his study of the relation between temperature and growth of *Phytophthora*, a genus closely related to *Pythium*.

It is readily seen that the behavior of conspecific isolates is most uniform at their upper temperature limit; the minimum and optimum values are more variable. The species may be segregated into groups, separation being based upon maximum temperature tolerance.

Growth occurred at 43° C. in all cultures of *Pythium aphanidermatum*, *P. deliense*, *P. helicoides*, *P. myriotylum*, *P. butleri*, and *P. aphanidermatum* var. *hawaiiensis*. *P. butleri* and *P. aphanidermatum* var. *hawaiiensis* are considered synonymous with *P. aphanidermatum* for morphological reasons. The temperature response is presented here as evidence of their physiological similarity.

Some isolates of *Pythium aphanidermatum* are capable of growing at 46° C.; no other species of *Pythium* grows at this temperature.

Another group of isolates grew at 40° C. but not at 43° C.; this included *Pythium acanthicum*, *P. afertile*, *P. arrhenomanes*, *P. echinulatum*, *P. graminicolum*, *P. hypogynum*, *P. oedochilum*, *P. oligandrum*, *P. periilum*, *P. periplocum*, and *P. plerosporon*. Only six of the fifteen isolates of *P. arrhenomanes* grew at 40° C.; the remainder failed to grow at 40° C., but grew at 37° C. Likewise, only three of nine cultures of *P. graminicolum* grew at 40° C., the balance having their maxima at 37°. Two cultures of *P. oligandrum* did not grow at 40° even though a single isolate did.

For morphological reasons a culture received by the writer as *Pythium echinulatum* is considered synonymous with *P. acanthicum;* the temperature values for the two isolates are identical.

The majority of *Pythium* spp. fall in the group having a maximum temperature of 37° C. These species are: *P. acanthophoron*, *P. araiosporon*, *P. aristosporum*, *P. arrhenomanes*, *P. arrhenomanes* var. *canadensis*, *P. arrhenomanes* var. *hawaiiensis*, *P. arrhenomanes* var. *philippinensis*, *P. artotrogus*, *P. complens*, *P. debaryanum*, *P. debaryanum* var. *pelargonii*, *P. epiphanosporon*, *P. euthyhyphon*, *P. fabae*, *P. graminicolum*, *P. hyphalosticton*, *P. indigoferae*, *P. irregulare*, *P. leiohyphon*, *P. paroecandrum*, *P. perniciosum*, *P. piperinum*, *P. polyandron*, *P. polymastum*, *P. rhizophthoron*, *P. salpingophorum*, *P. spaniogamon*, *P. spinosum*, *P. teratosporon*, *P. thysanohyphallon*, and *P. ultimum*.

Pythium arrhenomanes and *P. graminicolum*, though previously listed as developing slightly at 40° C., are more properly grouped with species having a maximum temperature of 37° C.

The three varieties of *Pythium arrhenomanes* and *P. epiphanosporon*, *P. hyphalosticton*, *P. leiohyphon*, *P. leucosticton*, *P. polyandron*, *P. rhizophthoron*, *P. spaniogamon*, and *P. thysanohyphallon* are all morphologically

identical and considered synonymous with *P. arrhenomanes*. The temperature-growth relations of these species are likewise identical; their temperature values are cited as evidence of their physiologic similarity.

Pythium complens and *P. monospermum* have similar temperature values attesting their physiologic synonymity; these two species are also morphologically indistinguishable.

Pythium teratosporon compares favorably with *Phytophthora drechsleri* in its temperature-growth requirements, with which it is now considered synonymous.

Pythium araiosporon, *P. debaryanum* var. *pelargonii*, and *P. fabae* exhibit temperature values comparable with those of *P. debaryanum*, which they resemble in their general growth habit. *P. araiosporon*, *P. debaryanum* var. *pelargonii*, and *P. fabae* are similar in their morphology and are treated as synonymous with *P. debaryanum*.

A smaller group of species have 34° C. as their limiting temperature. These are: *Pythium allantocladon*, *P. anandrum*, *P. ascophallon*, *P. complectens*, *P. diameson*, *P. dissotocum*, *P. intermedium*, *P. mamillatum*, *P. oryzae*, *P. polycladon*, *P. polycladon* var. *chamaihyphon*, *P. polymorphon*, *P. pulchrum*, *P. rostratum*, *P. splendens*, *P. torulosum*, and *P. vexans*.

Morphologically, *Pythium allantocladon*, *P. ascophallon*, *P. complectens*, and *P. vexans* are identical and must be considered synonymous species. *P. vexans*, having priority in description, is maintained as the valid binomial. The temperature values are presented as evidence of the physiologic similarity of these organisms.

For morphological reasons, *Pythium dissotocum* and *P. oryzae* are considered identical, *P. dissotocum* being designated as the valid nomen. The temperature-growth responses of these two organisms are identical and are cited here as additional evidence of synonymy.

A relatively few species comprise the group having 31° C. as their maximum temperature. These are *P. mastophorum*, *P. megalacanthum*, *P. sclerotiechum*, *P. tardicrescens*, and *P. volutum*.

Though the optimum temperature varies within a group of isolates of a single species, in general it may be said that the optimum temperature is usually about 10° below the maximum.

No generalizations may be made with regard to the minimum temperatures owing to the extreme elasticity in the range of temperature toleration of the various species.

There are several species which are able to grow at 1° C. These are: *Pythium afertile*, *P. anandrum*, *P. debaryanum*, *P. dissotocum*, *P. hypogynum*, *P. intermedium*, *P. mamillatum*, *P. plerosporon*, and *P. ultimum*.

Pythium acanthophoron is unique in being unable to grow at temperatures below 13° C.

It is interesting to note that isolates of a species from different climes have identical temperature values. This is well exemplified in *Pythium aphanider-*

matum, *P. arrhenomanes*, *P. graminicolum*, *P. irregulare*, *P. myriotylum*, *P. periplocum*, *P. ultimum*, and *P. vexans* (including synonyms). Apparently the climatic source of an isolation does not determine its ability to develop at a given temperature. As a specific example, cultures of *P. arrhenomanes* from Mauritius, Hawaii, and various parts of the United States are all capable of growing at 7° C. Similarly, isolations of *P. splendens* from Hawaii, Malaya, and the United States are capable of mycelial development at 7° C.

Literature relevant to the temperature requisites of *Pythium* spp. is rather limited so far as number of species is concerned. Gottlieb and Butler (1939) report that *P. aphanidermatum* does not grow at 5° C., that maximum mycelial development takes place at 37°, with only slight development at 45°. Tasugi and Takatuzi (1935) give the cardinal points as 10°, 30°, and 40° C. Wager (1931) states the optimum temperature to be 35° and the maximum 45°; no growth occurred at 5° C.

According to Vanterpool (1938), *Pythium aristosporum* grows most rapidly at 30° C., exhibiting only a trace of growth at 35°; no minimum temperature is presented. According to the writer's observations, the optimum temperature ranges between 25° and 31°, with somewhat better growth at 28° C. The maximum is about 2° higher than that recorded by Vanterpool.

Rands and Dopp (1934) report *Pythium arrhenomanes* capable of growing over a range of temperatures from 6° to 38° C., with the optimum about 30°. Vanterpool indicates that optimum temperature for growth of *P. arrhenomanes* is 30°, the maximum 35°; no minimum is given. Several isolates of the writer's collection grew at 4°; the optimum and maximum values are similar to those of Rands and Dopp.

Braun (1925) reports the cardinal temperatures of *Pythium debaryanum* as 6°, 27°, and 35.5° C. *P. debaryanum* var. *pelargonii*, described by Braun, has a minimum of 3°, an optimum of 30° and a maximum of 35.5°. Braun distinguishes this new variety from *P. debaryanum*, in part, by its lower minimum temperature. As previously indicated, no degree of significance can be attached to the minimum and optimum temperature values because they vary somewhat in conspecific isolates. Braun's use of the minimum temperature as an accessory factor in segregating his variety from the species is questionable; the writer does not consider it a valid criterion for separation. Though Braun points out some morphologic differences between the species and the variety, they are not believed sufficiently great to retain *P. debaryanum* var. *pelargonii* as a valid nomen. Saksena (1935) reports *P. debaryanum* to have an optimum temperature of 30° C. and a maximum of 35°.

According to Saksena, *Pythium deliense*, though able to grow at 15° C., cannot grow at 10°. The optimum temperature for growth is 35°; the maximum is stated to be intermediate between 40° and 45°.

Vanterpool (1938) reports the optimum temperature of *Pythium graminicolum* to be 25° C.; the maximum is coincidental with the optimum. No

instances of this sort have been observed among the isolates of *P. graminicolum* used in this study.

An incomplete study of the relation of temperature to growth of *Pythium indigoferae* by Saksena reveals the optimum of the fungus to be about 30° C., the maximum about 35°; no minimum value is recorded.

Younkin and Melhus (1939) report the optimum temperature of *Pythium irregulare* as 30° C., stating further that no growth occurred at 0° and 40°.

Saksena records *Pythium mamillatum* as having an optimum temperature for growth of 30° C. and a maximum of 35°; no minimum value is given.

The only published work dealing with the temperature values of the type species of the genus, *Pythium monospermum*, is that of Ito and Tokunaga (1933). They state that the optimum temperature of this fungus lies between 28° C. and 32°. No minimum or maximum temperatures are presented.

The temperature-growth values published by Harter and Whitney (1927b) for *Pythium scleroteichum* are not in harmony with those recorded by the writer. Harter and Whitney list the minimum as 8°, optimum 29°, and maximum 38.5° C.; the writer's values are: minimum 10°, optimum 25°, and maximum 31°. A comparison of the type culture with the Harter and Whitney fungus was not possible.

Sawada and Chen (1926) report the optimum temperature for the growth of *Pythium spinosum* as 30° C.; no further values are given.

Braun states the minimum, optimum, and maximum temperatures for the growth of *Pythium splendens* are 11°, 30°, and 37.5° C., respectively.

Vanterpool reports that *Pythium tardicrescens* is able to grow over a temperature range of 15° to 30°, with the optimum near 25° C. The writer was able to grow the fungus at temperatures ranging from 4° to 31°, with the optimum about 25° C. In the same paper, Vanterpool gives data indicating that *P. volutum* grows at 15° C. and 30°, but not at 35°; the optimum is given as 25°. A culture of *P. volutum* received from Vanterpool grew at 1° C. and 31°; the optimum growth occurred at 25°.

The temperature values of *Pythium ultimum* listed above in table 1 are in accord with reports of other investigators. Jones (1935) reports a minimum temperature value of approximately 4°, an optimum of 28°, and a maximum of 40° C. Likewise Wager (1931) has found the minimum temperature of *P. ultimum* to be rather low, about 4°. The optimum was 30° and the maximum about 40°. According to Pirone *et al.* (1933), the minimum value is somewhat lower than 9°, the optimum approximately 30°, and the maximum 38°. Alexander, Young, and Kiger (1931) report the optimum temperature of *P. ultimum* to be from 25° to 30°, the minimum about 10°; no maximum value is given.

In summation it may be said that temperature-growth relations are a specific feature and may be used as a criterion for the identification of species. The utilization of the ability of a species to grow at certain temperatures is particularly helpful as an adjunct to morphological characteristics in specific

identification. The temperature-growth relations cannot, however, be used to distinguish between species possessing filamentous or spherical sporangia, since there is no correlation between cardinal temperatures and morphologic characters.

TAXONOMY OF THE GENUS

Pringsheim (1858) created the genus *Pythium* in 1858, placing it in the family Saprolegniaceae. His description of the genus is as follows:

"*Pythium* n.g. Schwarmsporen aussen vor der Oeffnung der Sporangien aus deren Inhalt gebildet, sich nicht hautend. Schlauche die enterleerten Sporangien weder durchwachsend noch seitliche Sporangien treibend. Oosporen einzeln in jedem oogonium."

Pythium monospermum and *P. entophytum* were the first described species. With the subsequent transfer of *P. entophytum* to *Lagenidium entophytum* by Zopf (1890), *P. monospermum* became the type species.

Cornu (1872) includes *Pythium* in his treatise on the Saprolegniaceae published in 1872. In 1881 de Bary (1881b) published a series of articles dealing with the genera *Artotrogus*, *Peronospora*, *Phytophthora*, and *Pythium*. He points out the similarity of the genera, indicates their probable interrelationships and concludes that they should be placed in the family Peronosporaceae.

In 1888 Berlese and de Toni in Saccardo's *Sylloge Fungorum* (1888) return to Pringsheim's placement of the genus *Pythium* in the Saprolegniaceae. Four years later a monograph on the genus was presented by Fischer (1892) in which he refers *Pythium* to the Peronosporaceae. This work is noteworthy for the creation of the subgenera *Aphragmium*, *Nematosporangium*, and *Sphaerosporangium* and the sections *Orthosporangium* and *Metasporangium*. The subgenera *Aphragmium* and *Nematosporangium* represent groups of species possessing filamentous sporangia. *Aphragmium* is distinguished from *Nematosporangium* as devoid of a septum delimiting the sporangium from the mycelium. The subgenus *Sphaerosporangium* embraces species producing spheroidal sporangia cut off from the sporangiophore by a septum. The author describes the sporangial habits found in the subgenus *Sphaerosporangium: Orthosporangium* includes species in which the sporangium remains attached to the sporangiophore during zoospore formation; in *Metasporangium* the sporangia may be either fixed or deciduous with zoospore production occurring in either case, or the sporangia may fail to form zoospores and may germinate by means of germ tubes.

Schröter (1897) in 1897 placed the genus *Pythium* in a newly created family, the Pythiaceae, assigned to the order Saprolegniales. The subgenus *Nematosporangium* is elevated to generic rank and included in the Pythiaceae. Schröter designates *Nematosporangium* as having filamentous sporangia and *Pythium* as having spherical or limoniform sporangia. Two subgenera,

Aphragmium Fischer and *Eunematosporangium* (*Nematosporangium* Fischer), are included in the newly elevated genus *Nematosporangium*. The subgenus *Aphragmium* is retained in Fischer's sense while *Eunematosporangium* is considered synonymous with the subgenus *Nematosporangium* Fischer. *Pythium*, according to Schröter's treatment, is synonymous with Fischer's subgenus *Sphaerosporangium*. Schröter also presents two new subgenera for his genus *Pythium: Eupythium*, including species with smooth-walled oogonia, and *Artotrogus*, including species with echinulate-walled oogonia.

The writer favors abandonment of the subgenera *Aphragmium* and *Nematosporangium* and the two sections *Orthosporangium* and *Metasporangium* and suggests that the use of subgenera and sections in the genus *Pythium, sensu* Pringsheim, be discontinued. The presence or absence of a septum delimiting a sporangium cannot be considered a valid taxonomic criterion; the character is too variable. The subgenus *Sphaerosporangium* is sufficiently descriptive but does not aid materially in clarification. The mode of sporangial germination is largely controlled by conditions existing in the immediate environment. The sporangium of most *Pythium* spp. may germinate either by the formation of zoospores or by the production of germ tubes. When sporangia are introduced into fresh running water they nearly invariably germinate by the production of zoospores. If similar sporangia are placed in agar blocks without any surface water other than the water film naturally present, the sporangia invariably germinate by the formation of germ tubes. These observations are true not only for the species included in Fischer's *Sphaerosporangium*, but in his *Aphragmium* and *Nematosporangium* as well. Utilization of the mode of sporangial germination, which may be regulated by environmental conditions, should be avoided as a taxonomic feature.

Schröter's treatment of the genus is questionable in many respects. His inclusion of *Pythium monospermum* in *Nematosporangium* is irreconcilable with Pringsheim's delineation of *Pythium*. *P. monospermum* is the type species of the genus *Pythium* created by Pringsheim. Schröter's delineation of *Pythium* is identical with Fischer's subgenus *Sphaerosporangium* created to include species possessing spherical or limoniform sporangia. The adoption of the genera *Nematosporangium* and *Pythium, sensu* Schröter, seems unjustifiable because they are in direct opposition to the genus as originally described by Pringsheim. However, if the genus *Pythium* is to be divided into two groups following Schröter's plan, *Nematosporangium* would be embraced in the genus *Pythium* since *Pythium* was described first, making abandonment of *Nematosporangium* mandatory; a new genus would have to be proposed to replace *Pythium, sensu* Schröter.

Butler in his monograph on *Pythium* published in 1907 follows Fischer's treatment in retaining the various species within this single genus. Butler considers the subgenus *Nematosporangium* of doubtful validity, grouping all species possessing filamentous sporangia within the subgenus *Aphragmium*.

In 1930 Sideris (1930) proposed to revive the taxonomic plan proposed by Schröter. Sparrow (1931c) published a criticism of Sideris' paper, suggesting the replacement of the genus *Nematosporangium* by *Pythium* and the transference of *Pythium* spp. possessing inflated filamentous sporangia to the genus *Rheosporangium*, erected by Edson (1915b). Sparrow further proposed either that *Pythium* spp. possessing spherical or limoniform sporangia and all *Phytophthora* spp. be placed in *Sphaerosporangium*, elevating it to generic rank, or that *Pythium* spp. be placed in *Phytophthora*. These suggestions contribute little to the solution of the problem. The genus *Phytophthora*, though related to *Pythium* in the broader sense, comprises a group of species easily distinguishable from *Pythium*. Further, *Pythium* spp. with filamentous or inflated filamentous sporangia exhibit too many common characteristics to permit valid generic segregation.

The mode of zoospore production has been the principal distinguishing character for the separation of the genera *Pythium* and *Phytophthora*; this feature may be retained as a criterion of generic segregation despite recurring criticism if its value and limitations are thoroughly understood and appreciated. Under suitable environmental conditions the sporangia of the genus *Pythium* give rise to an emission tube capped by a vesicle; the undifferentiated contents of the sporangium pass into the vesicle and there through a series of cleavages is differentiated into zoospores. The vesicle then ruptures and the zoospores are set free. In *Phytophthora* zoospores are produced within the sporangium in the absence of any vesicle; liberation is accomplished through disruption of the sporangium wall, or through dissolution of a differentiated region, the papilla. Rare instances are on record wherein the sporangia of *Phytophthora* have given rise to vesicles. It must be borne in mind that in these aberrant cases the protoplasm does not flow into the vesicle in an undifferentiated state, but rather already differentiated into zoospores. Inasmuch as the production of a vesicle is an asexual form of reproduction and as such should not be considered an unfailing process, the use of the vesicle for generic segregation should not be over-emphasized; this does not preclude its use as a character indicative of generic distinction or for convenience in separating the genera. There are several other characters which serve to distinguish further *Pythium* from *Phytophthora*. The amphigynous type of antheridium predominant in the genus *Phytophthora* is unique and not encountered in the genus *Pythium;* that the antheridium is a component part of the sexual phase can be considered a valid criterion for separation. The two species of *Phytophthora* which possess paragynous antheridia are readily separated from *Pythium* species possessing similar antheridia. Sporangiophore branching is unusual in *Pythium* and not uncommon in *Phytophthora*. The habits of growth of *Pythium* and *Phytophthora* are different enough for general macroscopic distinction. Though there is no one infallible feature for generic segregation of these two genera, there are a

number of characteristics which make separation feasible, and though difficult to outline in abbreviated form, in practice separation is easily done.

In this taxonomic study the generic tenets of Butler (1907) and Matthews (1931) are followed and the genus is retained in the older and broader sense; the taxonomic study presented by Sideris (1930), patterned after Schröter's, is not considered herein.

KEY TO THE SPECIES

For species not included in the key refer to "Doubtful Species."

Sporangium filamentous.
- Sporangium undifferentiated from vegetative hypha; not inflated.
  - Sexual reproduction present.
    - Oogonium smooth.
      - Antheridium delimited by septum.
        - Oospore smooth.
          - Oospore plerotic.
            - Antheridium monoclinous or diclinous, one to two per oogonium ..... 1. *P. monospermum*
            - Antheridium diclinous, one per oogonium ..... 2. *P. marinum*
          - Oospore aplerotic.
            - Oospore wall inspissate.
              - Catenulate spherical asexual reproductive bodies present ..... 3. *P. perniciosum*
              - Catenulate spherical asexual reproductive bodies absent.
                - Antheridium monoclinous, occasionally diclinous.
                  - Antheridial cells one to five, mostly two to three per oogonium, of autonomous origin ..... 4. *P. dissotocum*
                - Antheridium diclinous, never monoclinous.
                  - Antheridial cells one, rarely two per oogonium, of autonomous origin ..... 5. *P. gracile*
                  - Antheridial cells one to four per oogonium, as lateral prolongations of a single antheridial branch ..... 6. *P. adhaerens*
            - Oospore wall not inspissate.
              - Antheridium monoclinous or diclinous, one to five per oogonium ..... 7. *P. angustatum*
              - Antheridium diclinous, never monoclinous ..... 8. *P. apleroticum*
          - Oospore wall reticulate ..... 9. *P. dictyosporum*
        - Antheridium not delimited by septum ..... 10. *P. tenue*
      - Oogonium papillate ..... 11. *P. papillatum*
    - Sexual reproduction absent ..... 12. *P. afertile*
- Sporangium somewhat differentiated from vegetative hypha; inflated.
  - Sexual reproduction present.
    - Oogonium smooth.
      - Oospore plerotic.
        - Catenulate spherical asexual reproductive bodies present ..... 13. *P. catenulatum*
        - Catenulate spherical asexual reproductive bodies absent.
          - Antheridium monoclinous; origin proximal to oogonium.
            - Antheridial cells one to two per oogonium; not greatly inflated, allantoid-clavate; oogonium small, 12.0 to 19.0 μ in diameter ..... 14. *P. torulosum*
            - Antheridial cells two to six per oogonium; inflated, crook-necked-clavate; oogonium large, 16.5 to 28.6 μ (Subr.), often larger, 24 to 36 μ in diameter ..... 15. *P. graminicolum*
          - Antheridium diclinous; origin not proximal to oogonium.
            - Antheridial cells arising from separate antheridial branches.

Antheridial branches simple; antheridial cells few, one to two per oogonium.....16. *P. inflatum*
Antheridial branches frequently divided; antheridial cells many, up to 25 per oogonium.....17. *P. arrhenomanes*
Antheridial cells arising from a single antheridial branch...18. *P. periilum*
Oospore aplerotic.
Antheridium monoclinous, occasionally diclinous.
Antheridial branch usually straight; oogonial branch curved toward the antheridium.
Oogonium and antheridium frequently formed in connection with lateral sporangial complexes.....19. *P. indigoferae*
Oogonium and antheridium never formed in connection with lateral sporangial complexes.....20. *P. deliense*
Antheridial branch rarely straight; oogonial branch not curved toward the antheridium.
Antheridial cell typically intercalary, sometimes terminal, inflated; one to two per oogonium.....21. *P. aphanidermatum*
Antheridial cell typically terminal, never intercalary, not greatly inflated; one to six, mostly two to three, per oogonium.....22. *P. tardicrescens*
Antheridium diclinous, occasionally monoclinous.
Antheridial branch frequently helicoid about the oogonial branch.....23. *P. volutum*
Antheridial branch not helicoid about the oogonial branch.
Origin of antheridial branch proximal to oogonium; vegetative prolongations rare; antheridial cells crook-necked, with apical contact with oogonium.....24. *P. aristosporum*
Origin of antheridial branch not proximal to oogonium; vegetative prolongations common; antheridial cells crook-necked, with basal and apical contact with the oogonium
25. *P. myriotylum*
Oogonium echinulate.....26. *P. periplocum*
Sporangium spheroidal.
Sexual reproduction present.
Oogonium smooth.
Oospore smooth.
Oospore plerotic.
Sporangium proliferous.....27. *P. salpingophorum*
Sporangium not proliferous.
Antheridium absent.....28. *P. conidiophorum*
Antheridium present.
Antheridium monoclinous or hypogynous.
Antheridial cell hypogynous, fertilization tube long and tenuous.....29. *P. hypogynum*
Antheridial cell monoclinous, originating in close proximity to the oogonium, may be reduced to a hypogynous cell or short lateral process, fertilization tube short and stout.
30. *P. rostratum*
Antheridium monoclinous or diclinous, not hypogynous....31. *P. iwayamai*
Oospore aplerotic.
Sporangium proliferous.
Oospore wall inspissate.
Oospore containing a single reserve globule.
Antheridium typically monoclinous, rarely diclinous....32. *P. proliferum*
Antheridium typically diclinous; rarely monoclinous...33. *P. marsipium.*
Oospore containing several reserve globules.
Sporangium spherical.....34. *P. polytylum*
Sporangium ovoid to obovoid.

Antheridial cell elongate, cylindrical, curved, regular in contour....35. *P. helicoides*
Antheridial cell elongate, cylindrical, curved, irregular and wavy in contour.
Oogonia typically acrogenous....36. *P. oedochilum*
Oogonia typically laterally and tangentially intercalary....37. *P. palingenes*
Oospore wall not inspissate....38. *P. nagaii*
Sporangium not proliferous.
Antheridium absent....39. *P. anguillulae-aceti*
Antheridium present.
Antheridium typically hypogynous, rarely monoclinous...40. *P. pulchrum*
Antheridium typically monoclinous or diclinous, never hypogynous.
Antheridial branch falcate, sigmoid....41. *P. polymorphon*
Antheridial branch not falcate, not sigmoid.
Antheridium typically sessile, originating immediately adjacent to the oogonium.
Oospore wall inspissate....42. *P. ultimum*
Oospore wall not inspissate....43. *P. paroecandrum*
Antheridium typically stalked, not originating immediately adjacent to the oogonium.
Sporangium terminal....44. *P. splendens*
Sporangium terminal or intercalary.
Antheridium crook-necked, clavate, the apex bell-shaped, closely appressed to the oogonium and frequently fused with it....45. *P. vexans*
Antheridium crook-necked, clavate, the apex obtuse, narrowly applied to the oogonium....46. *P. debaryanum*
Oospore wall reticulate....47. *P. cystosiphon*
Oogonium echinulate.
Oospore plerotic.
Contiguous sporangia present....48. *P. acanthicum*
Contiguous sporangia absent.
Oogonial protuberances short, conical....49. *P. mamillatum*
Oogonial protuberances long, digitate....50. *P. spinosum*
Oospore aplerotic.
Contiguous sporangia present....51. *P. oligandrum*
Contiguous sporangia absent.
Sporangium proliferous....52. *P. megalacanthum*
Sporangium not proliferous.
Sporangium papillate....53. *P. anandrum*
Sporangium not papillate.
Antheridium typically hypogynous, rarely stalked....54. *P. echinulatum*
Antheridium typically stalked, never hypogynous.
Oogonial protuberances mammiform.
Sporangium regular in contour, devoid of protuberances. 55. *P. mastophorum*
Sporangium irregular in contour, possessing dome-shaped protuberances....56. *P. polymastum*
Oogonial protuberances not mammiform....57. *P. irregulare*
Sexual reproduction absent.
Sporangium proliferous.
Sporangium papillate.
Sporangium prolate ellipsoidal, vesicle sessile....58. *P. undulatum*
Sporangium spherical, vesicle stalked....59. *P. carolinianum*
Sporangium not papillate....60. *P. diacarpum*

Sporangium not proliferous.
Sporangia catenulate ..... 61. *P. intermedium*
Sporangia not catenulate ..... 62. *P. elongatum*
Sporangium unknown.
Oogonium smooth ..... 63. *P. scleroteichum*
Oogonium echinulate.
Antheridium hypogynous, never stalked ..... 64. *P. artotrogus*
Antheridium typically stalked, occasionally hypogynous.
Oogonial protuberances acute ..... 65. *P. echinocarpum*
Oogonial protuberances obtuse ..... 66. *P. acanthophoron*

DESCRIPTION AND DISCUSSION OF THE SPECIES

1. PYTHIUM MONOSPERMUM Pringsheim, Jahrb. Wiss. Bot. 1: 284–306. 1858.

Pythium gracile de Bary, Jahrb. Wiss. Bot. 2: 169–192. 1860.
Pythium reptans de Bary, l.c.
Pythium fecundum Wahrlich, Ber. Deuts. Bot. Ges. 5: 242–246. 1887.
Pythium complens Fischer in Rabenhorst, Kryptogamen-Flora 1: 398–399. 1892.

Hyphae measuring 1.6 to 7.3 μ, mostly 2 to 5 μ, in diameter, frequently including in addition to the cylindrical portion, a number of swollen, bud-like lateral outgrowths. Sporangia filamentous, unbranched or branched, 80 to 170 μ long, 2 to 5 μ in diameter, delimited by a septum. Zoospores few to 60 or more in number, reniform, 3.4 to 6.3 μ wide, 5.3 to 8.8 μ long. Oogonia spherical, thin and smooth-walled, usually intercalary, though frequently terminal or subterminal, 14.2 to 23.7 μ, mostly 15.8 to 21.9 μ in diameter. Antheridia usually one, occasionally two per oogonium, of monoclinous or diclinous origin; antheridial cell slightly inflated, clavate and crook-necked. Oospores single, plerotic, wall inspissate, a single reserve globule and a prolate ellipsoidal refringent body usually embedded in the granular protoplasm.

Originally described as a saprophyte on insect cadavers in water, Germany.

Pythium monospermum and *P. entophytum* were originally described by Pringsheim as the type species of the genus. Since Zopf's transference (1890) of *P. entophytum* to the genus *Lagenidium*, *P. monospermum* remains the type species.

It is indeed curious that *Pythium* spp. with strictly filamentous sporangia like those described by Pringsheim should frequently be referred to as members of the *P. gracile* group, the group name based on a species described a few years later from an asexual stage indistinguishable from that of *P. monospermum*. There may be some reason for this treatment if the division is based on the parasitic behavior of the sundry related forms. Although *P. monospermum* is usually reported as a saprophyte from either insect cadavers or plant debris, the species is occasionally recovered from living plant material. *P. gracile* is more often recorded as a parasite, usually of algae. These two species may be distinguished readily by their sexual stages. In *P. monospermum* the oospores are plerotic, the antheridia both monoclinous and diclinous; in *P. gracile* the oospores are aplerotic, the antheridia diclinous.

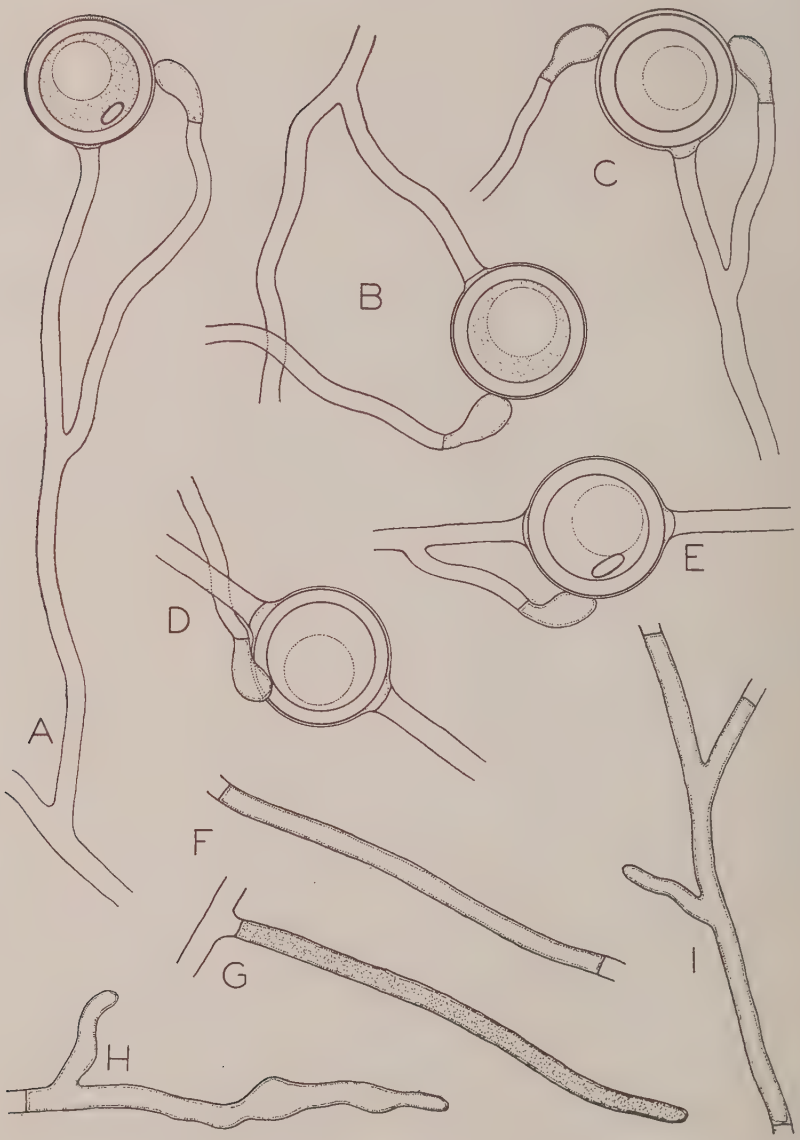

FIG. 1. *Pythium monospermum*. *A–E*, Sexual apparatus. *A*, Acrogenous oogonium with monoclinous antheridium and plerotic oospore. *B*, Acrogenous oogonium with diclinous antheridium. *C*, Acrogenous oogonium with both diclinous and monoclinous antheridia. *D*, Intercalary oogonium with diclinous antheridium. *E*, Intercalary oogonium with monoclinous antheridium. *F–I*, Typical filamentous sporangia.

Pythium monospermum and *P. marinum* both have plerotic, inspissate oospores. They may be distinguished morphologically by the origin and number of antheridia, diclinous and singular in *P. marinum*, monoclinous and diclinous, singular or plural in *P. monospermum*. They also may be easily segregated on the basis of their habitat, marine in *P. marinum* and fresh-water in *P. monospermum*. The sporangia of these species are indistinguishable.

Butler (1907) reports that *Pythium complens* Fischer was described to include *P. gracile*, *sensu* de Bary, and saprophytic *P. reptans* de Bary; the parasitic form of *P. reptans* de Bary properly belongs in *P. gracile*. Since *P. complens* is indistinguishable from *P. monospermum*, Butler places the saprophytic *P. reptans*, *P. gracile*, *sensu* de Bary, together with *P. complens* in *P. monospermum*. Butler follows Fischer (1892) in considering *P. fecundum* Wahrlich a synonym of *P. monospermum*. The description of *P. fecundum* presented by Wahrlich is almost identical with that of *P. monospermum*. The salient features of Wahrlich's description are:

Hyphae delicate, 2 to 5 μ, some threads larger, 4 to 5 μ, in diameter. Sporangia filamentous, 2 μ wide by 120 to 160 μ long. Vesicle formed in which 8 to 16 zoospores develop; zoospores are 4 μ broad, 6 μ long, laterally biciliate. Oogonia spherical, smooth and thin-walled, usually intercalary, occasionally subterminal or terminal. Antheridia one or two per oogonium, usually monoclinous when singular, when plural one usually of diclinous origin. Oospores, one to three, aplerotic, 12 to 14 μ in diameter.

Recently Rands and Dopp (1938b) report the isolation of *Pythium complens* from sugarcane roots in Louisiana, U. S. A. In the same year Stevenson and Rands (1938) indicated the synonymity of *P. gracile*, *sensu* de Bary, with *P. complens*, but failed to recognize the synonymity of *P. complens* with *P. monospermum*. A study of a culture of *P. complens* received by the writer from Rands corroborates the contention of Butler that *P. complens* would be properly embraced in the binomial *P. monospermum* and not in *P. gracile*, *sensu* de Bary, which is also properly referred to as *P. monospermum*. Fischer recognized the close relationship between *P. complens* and *P. monospermum* when he stated: "Sollte die Bildung einer Sporangienquerwand sich spater herausstellen, so wurde *P. complens* wohl mit *P. monospermum* zu Vereinigen sein." It seems undesirable to maintain two distinct species on the basis of the presence or absence of a delimiting sporangial septum; characteristics of this kind are too variable to be utilized in specific segregation.

Schröter in de Wildeman (1895) reports that the principal difference between *P. complens* and *P. gracile* is that the former is purely saprophytic and unable to attack living algae, whereas *P. gracile* is capable of parasitizing the living cells of algae. The principal difference between these species does not lie in their potentialities as parasites; rather in their distinctly different morphological characteristics, a single, monoclinous antheridium and plerotic oospore in *P. complens* as contrasted with a single, or occasionally two, diclinous anteridium and an aplerotic oospore in *P. gracile*.

The cardinal temperatures for mycelial growth of *Pythium monospermum* are: minimum, approximately 4°, optimum 31° and maximum 37° C.

Pythium monospermum is reported occurring from animal debris in Germany by Pringsheim (1858), de Bary (1860), in France by Dangeard (1890–91); from animal and plant debris in Germany by Wahrlich (1887); from soil in Ireland by Butler (1907), in the United States by Harvey (1925, 1927, 1929) and Raper (1928); from soil and water in U. S. A. by Matthews (1931) and the author; from *Hordeum vulgare* L. in the United States by the author, from *Lepidium sativum* L. in India by Butler and Bisby (1931); from *Nicotiana tabacum* L. in Java by Raciborski (1900); from *Oryza sativa* L. in Japan by Ito and Tokunaga (1933); from *Persea Americana* Mill. in the United States by the author; from *Richardia aethiopica* L. in the Netherlands by Meurs (1928); from *Saccharum officinarum* L. in the United States by Rands and Dopp (1938a, b); from *Spinacia oleracea* L. in the Netherlands by Meurs, and from *Zingiber officinale* Roscoe in India by Butler and Bisby.

2. Pythium marinum Sparrow, Bot. Arkiv **8**: 1–24. 1934.

Hyphae measuring 2.5 to 3.5 μ in diameter, sparingly branched, intramatrical. Sporangia strictly filamentous, not inflated, extramatrical; producing 2 to 6 reniform, laterally biciliate zoospores 4.5 μ in width and 7.5 μ in length. Oogonia typically terminal on short lateral branches, spherical to ellipsoidal, smooth-walled, occasionally with a small apical papilla. Antheridia single, diclinous, clavate, 6 to 8 μ wide by 11 to 13 μ long, the apex tapering abruptly. Oospores plerotic, spherical to ellipsoidal, 13 to 20 μ by 15 to 21 μ, with a somewhat inspissate wall measuring 1.5 to 2 μ in thickness; germination not observed.

Saprophytic on dead fronds of *Ceramium rubrum* (Huds.) Ag., Denmark.

Material of this fungus was not available to the writer, the following discussion being based on Sparrow's paper in which he describes the species. As he mentions, this is not the first record of Pythium from Rhodophyceae. De Bary (1860) described *P. reptans* from a fresh water alga, *Bangia atropurpurea* (Roth) Agardh, but as only the asexual stage was seen considerable doubt exists as to the exact identity of the fungus. *P. reptans* is usually considered synonymous with *P. gracile* Schenk, *sensu* Butler.

Pythium marinum is reportedly a member of the *P. gracile* group, though differing considerably from *P. gracile* and closely related forms which not only have aplerotic oospores but frequently polyandrous oogonia and antheridia of monoclinous origin. *P. marinum* is unique at present in being the only member of the genus described from a marine habitat. Of the strictly filamentous sporangial forms, plerotic oospores are common to *P. marinum*, *P. monospermum*, and *P. papillatum*. *P. papillatum* has apandrous, papillate oogonia, being easily distinguishable from *P. marinum* which has monandrous, smooth oogonia. *P. monospermum* exhibits a closer relationship to *P. marinum* than does *P. papillatum*. In both of these species diclinous antheridia are present. Frequently either monoclinous or diclinous or occa-

sionally both types of antheridia are found in *P. monospermum*, while only diclinous antheridia are found in *P. marinum*. Oogonia of *P. monospermum* are more often intercalary than terminal, while those of *P. marinum* are nearly always terminal. There are no outstanding differences in the asexual apparatus and behavior of the latter two species, the development of the vesicle and zoospore formation being typical of the genus.

This species has so far only been reported from *Ceramium rubrum* in Denmark.

3. PYTHIUM PERNICIOSUM Serbinow, Scripta Bot. Hort. Univ. Imp. Petrop. 28: 1–47. 1912.

Hyphae measuring 5 to 9.5 μ in diameter, capable of breaking up into functional units, oidia. Sporangia filamentous, like hyphae, or originating from a swollen, sac-like structure on the hypha. Catenulate spherical reproductive bodies 17.4 to 30 μ in diameter also present, 3 to 5 in a series, which germinate by germ-tubes. Zoospores 8 to 16 in number, 8 to 12 μ in diameter. Oogonia spherical, smooth and thin-walled, acrogenous on short mycelial branches, 18.9 to 30.0 μ in diameter. Antheridia usually one, occasionally two, per oogonium, of monoclinous or diclinous origin; antheridial cell clavate, slightly curved, apical contact with oogonium. Oospores single, aplerotic, wall inspissate, measuring 18.1 to 23.5 μ in diameter; germination unknown.

Originally described as a parasite of tobacco seedlings, Russia.

The writer's observations are confined to the study of a single isolate of the fungus obtained from some rotted poinsettia cuttings, *Euphorbia pulcherrima* Willd., collected at Colma, California. The fungus studied agrees in every detail with the description presented by Serbinow.

Pythium perniciosum produces typical, strictly filamentous sporangia in agar cultures. When such cultures are irrigated with water the sporangia put forth delicate discharge tubes which soon form spherical, thin-walled vesicles at their apices. Serbinow reports seeing 8 to 10 zoospores in a vesicle; in several instances more than 30 zoospores were seen by the author.

Pythium perniciosum is easily distinguished from the other filamentous forms with aplerotic, inspissate oospores in possessing catenulate, spherical, asexual reproductive bodies. These resemble the oogonia, both in size and form. Oogonia, however, have never been observed in chains. It is probable that the catenulate asexual reproductive bodies may be frustrated oogonia. Ward (1883), Wahrlich (1887), Butler (1907) and more recently the writer (Tompkins *et al.*, 1939) have demonstrated that in several species the sexuality of incipient oogonia remains in doubt for a varying period of time. The catenulate bodies germinate under proper environmental conditions by means of germ tubes; germination with the production of zoospores has not been observed.

The occurrence of filamentous and spheroidal elements in the asexual apparatus in the genus *Pythium* is unusual. Drechsler (1929) questions the purity of the culture used by Serbinow as the basis for his description of

P. perniciosum. It is certain that pure cultures were used by the writer; the organism conformed with Serbinow's description in all respects.

The minimum temperature for vegetative growth of *Pythium perniciosum* is 4°, the optimum 28° to 31°, and the maximum 37° C.

Serbinow successfully inoculated the following hosts in addition to *Nicotiana rustica* L. and *N. tabacum* L. from which *Pythium perniciosum* was originally collected: *Amaranthus albus* L., *Atropa belladonna* L., *Barbarea arcuata* Rchb., *Brassica napus* L., *Camelina sativa* L., *Chenopodium* sp., *Datura stramonium* L., *Hyoscyamus niger* L., *Lepidium draba* L., *L. latifolium* L., *Linum usitatissimum* L., *Lycopersicon esculentum* Mill., *Sinapis arvensis* L., *S. orientalis* L., *Solanum dulcamara* L., *Thlapsi arvense* L., *T. montanum* L., and "young fern plants." Eristavi and Mordvintzeff (1930) report the recurrence of the seedling rot of *N. tabacum* caused by *P. perniciosum* in Russia. Van Eek (1938) states that this fungus is associated with a root rot of *Viola tricolor* L. in the Netherlands; Muller and van Eek (1939) report a root rot of *Hibiscus cannabinus* L. and *H. sabdariffa* L. in the Netherland East Indies due to this fungus.

4. Pythium dissotocum Drechsler, Jour. Wash. Acad. **20**: 398–418. 1930.

Pythium oryzae Ito and Tokunaga, Jour. Fac. Agr. Res. Hokkaido Imper. Univ. **32**: 201–233. 1933.

Hyphae measuring 1.5 to 7 μ, mostly 3.5 to 6 μ, in diameter. Sporangia typically undifferentiated hyphal elements, sparingly branched, occasionally including slightly swollen dactyloid laterals. Zoospores usually 10 to 75, though infrequently more than 100 in a vesicle, 8 to 9 μ in diameter when encysted, exhibiting repetitional emergence. Oogonia typically terminal though also intercalay, subspherical, measuring 12 to 33 μ, average 20.7 μ in diameter, smooth-walled, the delimiting septum or septa sometimes inserted beyond the oogonial contour. Antheridia usually monoclinous though also diclinous, 1 to 5 per oogonium, when plural each usually of autonomous origin, often sessile when monoclinous, when diclinous usually originating near the oogonium, measuring 5 to 8 μ in width and 6 to 16 μ in length. Oospores smooth, with a moderately thickened wall, aplerotic though almost filling oogonial cavity, 11 to 27 μ, average 17.6 μ, in diameter, containing a single reserve globule and subspherical or oblate ellipsoidal refringent body.

Isolated from roots of *Saccharum officinarum* L., Louisiana, U. S. A.

The paper in which the species was originally described contained no discussion of the fungus, being limited to the diagnosis. Drechsler recently (1940) discussed the fungus but limited his remarks to amplification of the diagnosis rather than including any comments of the relation of the species to congeneric forms. A culture of this fungus, isolated from sugar cane, was obtained for study. As stated by Drechsler the fungus resembles the general habit of *Pythium ultimum* when cultivated on rather rich substrates, but lacks the density of aerial mycelium encountered in *P. ultimum*. Whereas *P. ultimum* is a rapid growing species at room temperature, *P. dissotocum* grows somewhat more slowly. *P. dissotocum* forms asexual and sexual bodies

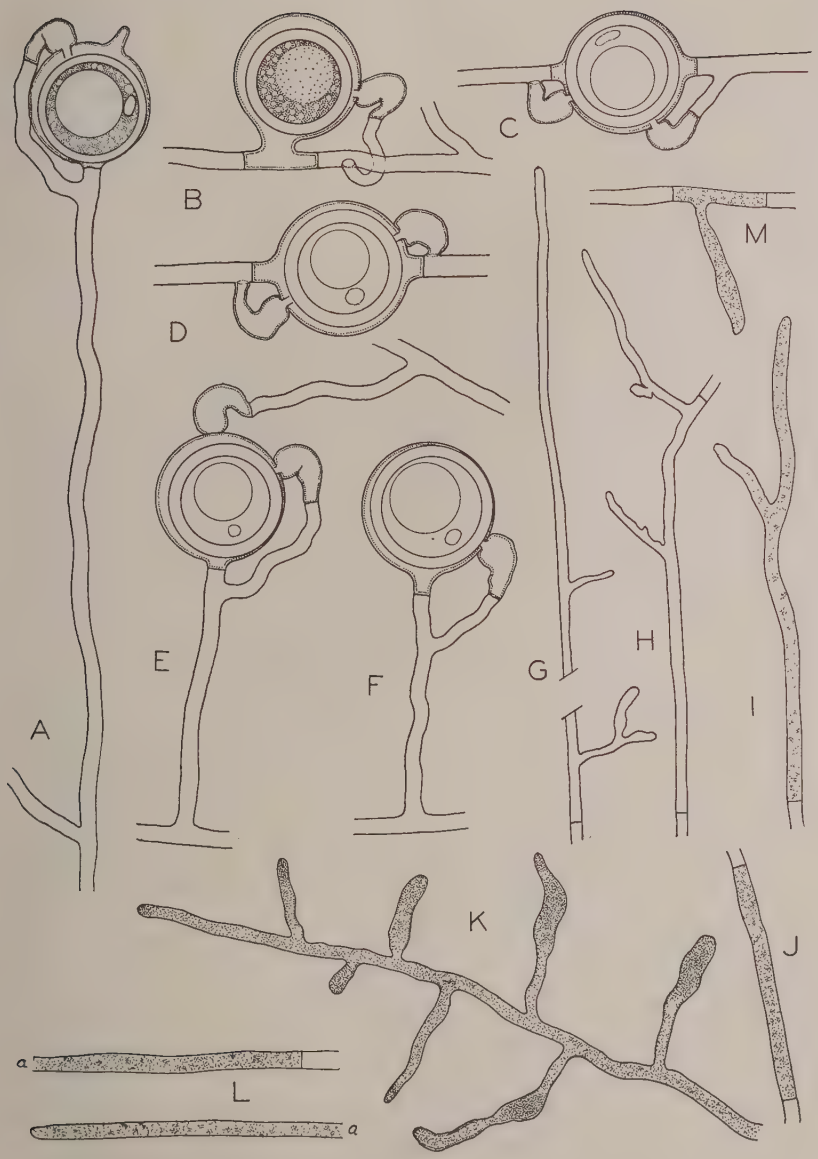

FIG. 2. *Pythium dissotocum*. *A–F*, Sexual apparatus. *G–M*, Filamentous sporangia. *K*, Type of development found in actively growing apical hyphae showing slight inflation of lateral lobes.

readily on suitable substrates. The asexual apparatus is indistinguishable from the vegetative hyphae when grown in a medium containing a paucity of free water. When agar blocks containing the fungus are properly irrigated evacuation tubes are produced at the top of which vesicles bearing zoospores develop. The evacuation tubes arise from the filamentous vegetative structures which may be considered sporangia. Apparently the conversion of a vegetative portion of the thallus into an asexual reproductive unit takes place without any preliminary visible change since evacuation tubes form in many instances from hyphal segments originally believed to be purely vegetative threads. Drechsler reports similar observations in his recent contribution concerning this species.

The sexual reproductive bodies are usually formed intramatrically, rarely on the extramatrical hyphae. The oogonia are more frequently intercalary, though are often terminal or medially disposed as noted in the diagnosis. The antheridia are usually monoclinous, though also diclinous and occasionally both. The antheridial cell is a distinctive feature of the species; it is crook-necked, inflated, breviform, and borne on a relatively short antheridial stalk or sessile. The tip of the antheridial cell is usually flattened where contacting the oogonium, in this respect differing from congeneric forms having short, inflated antheridia. The oospores conform with the description of these bodies in the diagnosis.

A careful study of an authentic culture of *Pythium oryzae* was undertaken in conjunction with the study of *P. dissotocum;* it is concluded that the two organisms must be considered synonymous. Since *P. dissotocum* was described three years prior to *P. oryzae*, *P. dissotocum* is retained as the valid binomial. A comparison of data relative to the two fungi substantiates the above conclusion. According to Drechsler, the sporangia of *P. dissotocum* consist of undifferentiated filaments, occasionally including swollen dactyloid laterals, simple or sparingly branched, 5 to 8 μ in diameter. Ito and Tokunaga (1933) describe the sporangia as "terminalibus, filiformibus, non ramosis, valde longis, 3 μ circiter crassis." Oogonia of *P. dissotocum* are 12 to 33 μ, av. 20.7 μ in diameter, acrogenous or intercalary; oogonia of *P. oryzae* are "terminalibus vel intercalaribus, 15 to 23 μ vel raro 13 μ in diameter." Antheridia of *P. dissotocum* compare favorably with the "antheridiis androgynis vel diclinous, singulis vel binis, abcaudicula per septum sectis, curvataclavatis vel oblongatis" of *P. oryzae*. Oospores of *P. dissotocum* measure 11 to 27 μ, mostly 15 to 21 μ, average 17.6 μ, in diameter compared with "12 to 20 μ vel raro 10 μ in diameter" in *P. oryzae*.

Further evidence of the synonymity of the species may be found in the data compiled from the study made by the writer. The measurements of *Pythium dissotocum* agree with those given by Drechsler. Some differences, however, were found in the measurements and description of *P. oryzae* as presented by Ito and Tokunaga and observed by the writer. The sporangia of *P. oryzae* are often not exclusively composed of strictly filamentous units

as depicted in the description, but often include a swollen, branched, digitate portion that is indistinguishable from the sporangia of *P. dissotocum*. No doubt the "frequenter multos ramos gemmiformes, breves, turgescentes, usques ad 10 μ crassis formantibus, interdum hyphae grandes gignentibus" described by Ito and Tokunaga as a part of the mycelium is in reality comparable to the companion part of the sporangium found in *P. dissotocum*. The description of the antheridia of *P. oryzae* is somewhat incomplete. Antheridia found in agar media vary from 1 to 5 in number and are borne on short antheridial branches which may be either monoclinous or diclinous in origin. Infrequently the antheridium is sessile; it is arched, inflated, the tip broadly applied to the oogonium, thus possessing a blunt apical aspect. These antheridia are indistinguishable from those of *P. dissotocum*. The oogonia and oospores vary in size more than is indicated in the description: oogonia 12.8 to 31.1 μ, mean 19.6 μ compared with 13 to 23 μ (no mean given) in diameter; oospores 9.7 to 25.6 μ, mean 16.7 μ compared with 10 to 20 μ (no mean given) in diameter.

As an adjunct to the above substantiating evidence for synonymity, reference may be made to the temperature-growth response of these two organisms. The cardinal temperatures for *Pythium dissotocum* are minimum 1°, optimum 28°, and maximum 34° C.; these are identical with those of *P. oryzae*. The growth habits of the two are identical.

Pythium dissotocum has been reported in the United States of America from *Saccharum officinarum* L. by Drechsler (1930a, 1940), Rands (1930), Rands and Abbott (1939) and Rands and Dopp (1938b); from *Beta vulgaris* L., *Pilea pumila* (L.) Gray, *Pisum sativum* L. and *Spinacia oleracea* L. in the U. S. A. by Drechsler (1940); from *Oryza sativa* L. in Japan by Ito and Tokunaga (1933) and Darker (1940).

5. PYTHIUM GRACILE Schenk, Verhandl. Phys.-Med. Ges. Wurzburg **9**: 12–31. 1859.

Pythium sp. Ward, Quart. Jour. Micr. Sci. **23**: 485. 1883.
Pythium diclinum Tokunaga, Trans. Sapporo Nat. Hist. Soc. **14**: 11–33. 1935.

Hyphae fine, measuring 1 to 5.6 μ, mostly 2 to 3.8 μ, in diameter. Sporangia filamentous, indistinguishable from the vegetative hyphae, branched or unbranched. Zoospores from 2 to 30 or more in a vesicle, reniform, 3 to 4 μ wide and 6 to 8 μ long. Oogonia usually formed intramatrically, spherical to ovoid, smooth, thin-walled, mostly acrogenous, occasionally subterminal or intercalary, 14.3 to 27.6 μ, mostly 15.7 to 24.2 μ, in diameter. Antheridia usually one, rarely two per oogonium, of diclinous origin, never monoclinous. Oospores single, aplerotic, wall inspissate, oospore measuring 11.1 to 21.3 μ, mostly 12.2 to 21.1 μ in diameter, containing a single reserve globule usually an ellipsoidal refringent body embedded in the granular protoplasmic content.

Originally described as parasitic on *Spirogyra nitida* (Dillw.) Link, *S. heeriana* Näg., and *Cladophora* sp., Germany.

The description given above is taken in part from Schenk's original work and supplemented with the observation of Fischer (1892), Butler (1907), and the writer.

Considerable confusion exists regarding this species. The fungus was originally described by Schenk in 1859 on the basis of the asexual stage; inasmuch as the sexual stage was not reported it is difficult to be certain of the exact identity of the species. Perhaps the ablest discussion of the species is that published by Butler in 1907 and Butler's scheme is followed here in the discussion of *Pythium gracile*.

A year after Schenk described *Pythium gracile*, de Bary (1860) described an organism indistinguishable from *P. gracile*, calling it *P. reptans*. In 1881 de Bary (1881a) described as *P. gracile, sensu* de Bary, another filamentous Pythium found as a saprophyte on insect cadavers in water. This fungus had originally been included in *P. reptans*. The new *P. gracile* is considered distinct from *P. gracile* Schenk due to its inability to infect living algae. In the same paper de Bary indicates that his *P. reptans* is more than likely *P. gracile* Schenk and suggests that the name *P. reptans* be discarded. Ward in 1883 described and figured a fungus which he considered synonymous with *P. gracile, sensu* de Bary. Differences were reported but were considered of minor importance. In the same paper Ward reports finding a fungus with oospores differing from those of his *P. gracile, sensu* de Bary, and lacking a sexual stage. It has been suggested that these oospores were those which Schenk failed to find in his study of *P. gracile*. Butler prefers to consider the fungus partially studied by Ward and a similar form studied by himself as *P. gracile* Schenk since other filamentous forms have since been provided with specific nomens, such as *P. tenue*, *P. monospermum* and others. The principal point in favor of Butler's action is expressed in his statement, "This appears to be more satisfactory than to add another to the names of Pythium parasites of algae."

The only morphological difference between *Pythium gracile, sensu* de Bary, and *P. monospermum* is that the sporangium of the former is not delimited by a septum. It is probable that the absence of a septum should not be used as a taxonomic feature. Fischer proposed *P. complens* in 1892 to replace the binomial *P. gracile, sensu* de Bary, since *P. gracile* Schenk takes precedence, *P. complens*, as already discussed, is correctly embraced in *P. monospermum*.

Very little work concerning this species has been done since Schröter's (1897) transference of *Pythium gracile* to *Nematosporangium gracile* and Butler's discussion, except the brief summarization of the species by Sparrow (1927).

Butler included three varieties in his concept of *Pythium gracile;* at present varieties *a.* and *b.* are the only ones considered valid. Variety *b.* was transferred to *P. diclinum* by Ito and Tokunaga; this disposition does not seem warranted. The similarity in size of oogonia and oospores of

P. diclinum as reported by Tokunaga (oogonia 18 to 25.2 μ and oospores 14.4 to 22.8 μ in diameter) and *P. gracile* var. *b.* as reported by Butler (oogonia 15 to 22 μ and oospores 13 to 20 μ, in diameter) is obvious and may indicate that Ito and Tokunaga were dealing with an organism identical with Butler's. The reason for segregating var. *b.* of Butler's *P. gracile* from *P. gracile* as now interpreted and describing it as a new species is not at all clear. Butler considered var. *b.* in conformity with the species despite its saprophytic habit. The oogonia and oospore measurements given by Butler for this variety certainly fall within the limits of the species as presented by Matthews (1931) and the observations of the writer. Specific segregation on a dimensional basis is of doubtful validity as previously indicated. The description of *P. diclinum* is identical with that of *P. gracile* with few exceptions: the hyphae and sporangia are of similar size and description, spherical, thin- and smooth-walled, occasionally subterminal ("... interdum prope apicem uno spiculo praeditis" of *P. diclinum*), antheridia strictly diclinous, oospores single and aplerotic with an inspissate wall. The differences in the description of the two species lie in the presence of "gemmiformes formantibus" in *P. diclinum*, which could be almost anything from appresoria to frustrated oogonia, and the generally plural antheridia in *P. diclinum*. There is typically a single antheridium in *P. gracile*, though there are infrequently two or possibly more; in *P. diclinum* there are "antheridiis 1–3 fere 2 quoque oogonia." This discrepancy in the difference in number of antheridia cannot be considered big or valid enough to warrant specific distinction. For these several reasons *P. diclinum* is considered synonymous with *P. gracile*.

Variety *c.* of *Pythium gracile, sensu* Butler, in roots and stems of *Zingiber officinale* Roscoe and in roots of *Ricinus communis* L. in water culture, has been transferred to *P. aphanidermatum;* discussion regarding this transference may be found under *P. aphanidermatum*.

The writer's observations are based on two isolates of the fungus, one from Missouri, the other from California. Both cultures agree with the concept of the species advanced by Butler.

Pythium gracile may be easily cultivated on a variety of nutrient agars. Reproductive structures are produced in moderate abundance. The species is separated from congeneric forms on the points set forth in the key: an aplerotic oospore with a thick wall, 2 to 2.5 μ thick, strictly diclinous antheridia, usually single though often two, the antheridial cell small, inflated-clavate, not greatly curved and narrowly applied to the oogonium, not blunt tipped as in *P. dissotocum*.

Pythium gracile is reported from *Bangia atro-purpurea* (Roth) Ag. (de Bary 1860), *Cladophora* sp. (Schenk 1859) in Germany, *Cladophora* sp. in France and Belgium by Schröter in de Wildeman (1895) and in England (Ward 1883), *Gossypium* sp. in Anglo-Egyptian Sudan (Andrews & Clouston, 1939), *Oryza sativa* L. (Ito & Tokunaga 1935) in Japan, plant debris (Butler

1907) in France and India, (Butler & Bisby 1931) in India, *Ricinus communis* L. (Sydow and Butler, 1907) in India, soil by the author in the United States of America, *Spirogyra* spp. (Sparrow 1933) in the U. S. A., *Spirogyra* sp. (Ward 1883) in England, (de Wildeman 1895) in France and Belgium, (Butler 1907) in India, (Matthews 1931) in the U. S. A., *Spirogyra crassa* Kütz. (Sparrow 1927) in the U. S. A., *S. heeriana* (Dill.) Link and *S. nitida* Näg. (Schenk 1859) in Germany, *S. porticalis* (Vauch.) Cleve (Saccardo *et al.*, 1904) in Alaska, *Triticum aestivum* L. by the author in the U. S. A., *Vaucheria* sp. (de Bary 1860) and *Vaucheria aversa* Hass. (Butler 1907) in Germany, *Xanthosoma sagittifolium* Schott. and *Colocasia antiquorum* Schott. in Gold Coast (Shepherd 1940), *Zingiber officinale* Roscoe (Sydow & Butler 1907) (McRae 1911) in India and (Parham 1935) in Fiji. Petersen (1910) reports *P. gracile* from "different algae" in Denmark. A *Pythium* sp. presumably identical with *P. gracile* is reported from *Triticum aestivum* L. roots in Italy by Petri (1930) and from *Carica papaya* L. in the Union of South Africa by Wager (1932a).

6. Pythium adhaerens Sparrow, Ann. Bot. **65**: 257–277. 1931.

Hyphae measuring 5 to 7.2 μ in diameter, intramatrical and extramatrical, forming numerous appressoria, usually 7.2 μ wide by 12 μ long. Sporangia undifferentiated from hyphae, filamentous; zoospores laterally biciliate, 6.5 μ wide by 10.8 μ long, 5.4 to 9 μ, average 7.2 μ, in diameter at encystment, exhibit repetitional emergence. Oogonia spherical, acrogenous or intercalary, smooth-walled, measuring 10.8 to 25.2 μ, average 17.5 μ in diameter. Antheridia diclinous, 1 to 4, typically borne as lateral branches of a single branch which often encircles the oogonium, seldom from several distinct branches, antheridial cell delimited, crook-necked, clavate, 7 μ wide by 15 μ long. Oospores aplerotic, spherical, measuring 7.2 to 21.6 μ, average 14.4 μ, in diameter, with a wall 2 to 2.5 μ thick, containing a single reserve globule; germination either direct or by zoospores.

Described as parasitic on *Rhizoclonium hieroglyphicum* (Ag.) Kütz., Mass., U. S. A.

No isolates of *Pythium adhaerens* were observed by the writer. This fungus lacks the somewhat compact complex of intercommunicating swollen dactyloid elements such as are present in *P. aphanidermatum*, *P. arrhenomanes* and related species. Appressoria are found in *P. adhaerens* which may be at first easily confused with the inflated digital elements of the species mentioned above. If, however, attempts are made to induce zoospore formation in these bodies, they will either produce further vegetative growth or remain unchanged, never producing zoospores.

The sexual apparatus of *Pythium adhaerens* differs somewhat from that of other species of the genus in that the antheridia, of which there are usually two to four per oogonium, arise from a single, diclinous hypha which surrounds the oogonium in a rather characteristic manner. The oogonia are typically intercalary or acrogenous. The oospores are aplerotic, germinating by the production of a branched germ tube; zoospores may also be produced.

Pythium adhaerens is closely related to *P. gracile*, both having aplerotic oospores and strictly diclinous antheridia. They differ decidedly, however, in the origin and disposition of their antheridial cells. In *P. adhaerens* the antheridial cells vary from one to four per oogonium and are all lateral prolongations of a single antheridial branch. *P. gracile*, on the other hand, usually has only one, rarely two, antheridial cells of autonomous origin.

Sparrow, in the same paper describing the species, adds that *Pythium adhaerens* is capable of parasitizing, when artificially inoculated, *Spirogyra crassa* Kütz., *Ulothrix zonata* Kütz., *Tolypothrix* sp., *Lycopersicon esculentum* Mill., *Cucumis sativus* L. and *Cucurbita moschata* Duchesne, thus presenting additional evidence that species described as algal parasites are not necessarily limited as parasites to algal hosts. Sparrow (1932) later added *Beta vulgaris* L., *Cucurbita pepo* L., *Pisum sativum* L., *Synedra* sp. and *Zea mays* L. as susceptible hosts.

7. PYTHIUM ANGUSTATUM Sparrow, Ann. Bot. **65**: 257–277. 1931.

Hyphae measuring 2 to 3.7 μ in diameter, intramatrical and extramatrical, rarely forming appressoria. Sporangia undifferentiated from hyphae, filamentous; zoospores laterally biciliate, 5 μ wide by 8.5 μ long, average 6.2 μ in diameter at encystment, exhibiting repetitional emergence. Oogonia spherical, rarely sac-like, acrogenous, smooth-walled, measuring 12.6 to 27.0 μ, average 19.8 μ, in diameter. Antheridia typically diclinous, rarely monoclinous, 1 to 5 per oogonium, the antheridial cells terminal on lateral distorted branches, delimited, crook-necked, measuring 5 μ wide and 8.5 μ long, the blunt apex making broad contact with the oogonium. Oospores single, rarely 2 to 4, aplerotic, measuring 10.8 to 25.2 μ, average 18.0 μ, in diameter, wall smooth and not inspissate, 1 to 1.8 μ in thickness, containing a single reserve globule. Oospore germinates by the production of a hypha which later may form sporangia.

Parasitic on *Spirogyra crassa* Kütz., Mass., U. S. A.

No cultures of *Pythium angustatum* were observed by the writer. Sparrow described this species as a companion species to *P. adhaerens*. In contrast to *P. adhaerens*, no appressoria are found in agar cultures of *P. angustatum*. This fact precludes any confusion with inflated filamentous sporangial forms such as *P. graminicolum*, *P. torulosum* and allied species.

Pythium angustatum demonstrates affinities toward *P. apleroticum* and *P. diclinum* from which it is principally distinguished by the disposition and origin of its antheridia. *P. apleroticum* and *P. diclinum* never have monoclinous antheridia, which are frequently displayed in *P. angustatum*. *P. apleroticum* possesses but a single antheridium, whereas *P. angustatum* exhibits a multiplicity. Though *P. angustatum* and *P. adhaerens* are closely related species and demonstrate a distinct relationship to *P. gracile*, they nevertheless retain their individuality.

In addition to parasitizing *Spirogyra crassa*, *Pythium angustatum* is also capable of infecting *Rhizoclonium hieroglyphicum* (Ag.) Kütz., *Oedogonium* sp. and *Zea mays* L. upon inoculation (Sparrow 1932).

8. PYTHIUM APLEROTICUM Tokunaga, Trans. Sapporo Nat. Hist. Soc. **14**: 11–33. 1935.

Hyphae tenuous, about 3 μ in diameter, intramatrical and extramatrical. Sporangia undifferentiated from hyphae, filamentous, usually terminal though sometimes lateral; zoospores reniform, laterally biciliate, 2 to 25 or more found in vesicle, measuring about 4.8 μ wide and 8.4 μ long. Oogonia spherical, acrogenous or intercalary, measuring 11 to 20 μ in diameter. Antheridia single, delimited by basal septum. Oospores single, aplerotic, spherical, measuring 9 to 17 μ in diameter, wall not inspissate, 0.6 to 0.8 μ thick.

Parasitic on *Spirogyra* sp., Sapporo, Japan.

Pythium apleroticum is not a well known species; any discussion of the fungus must necessarily be based exclusively on the works of Ito and Tokunaga in the absence of further information.

Pythium apleroticum is recorded as being allied with *P. gracile* but "differing in the small oogonium and thin oospore wall." A comparison of the measurements of *P. apleroticum* given by Tokunaga with measurements from the writer's collection is presented: *P. apleroticum*, oogonia 11 to 20 μ, oospores 9 to 17 μ in diameter; *P. gracile*, oogonia 14.3 to 27.7 μ, oospores 11.1 to 21.3 μ in diameter. These data substantiate the conclusions of Tokunaga. The difference in thickness of the oospore walls of the two species is perhaps more significant than the oogonial dimensions. The relationship between *P. apleroticum* and *P. angustatum* is probably closer than that between the species and *P. gracile* as stated by Ito and Tokunaga. The algal habit is common to both *P. apleroticum* and *P. angustatum;* perhaps of greater significance is the similarity in oospores, aplerotic ones with exceedingly thin walls being common to both. The inadequate description of the antheridium in *P. apleroticum* is compensated for by the authors in a brief discussion pointing out the striking similarity of their fungus to *P. gracile*, indicating the likeness in kind of antheridium. The single, diclinous antheridium of *P. apleroticum* is clearly distinguishable from the typically plural antheridia of *P. angustatum*, which are borne terminally on lateral, slender distorted branches of a single hypha, though infrequently from several discrete branches. Subsequent study of *P. apleroticum* may afford further distinguishing features not now recognized.

The fungus is only known from an unidentified species of *Spirogyra* collected in Sapporo, Japan.

9. PYTHIUM DICTYOSPORUM Raciborski, Bull. Acad. Int. Sci. Cracovie **1891**: 283–287. 1891; Krakow Nakt. Akad. Umietjet **24**: 1–9. 1892.

Hyphae measuring 1.8 to 2 μ in diameter, isodiametric, intramatrical, and extramatrical, capable of forming appressoria and occasionally irregular hyphal swellings. Sporangia undifferentiated from hyphae, filamentous; zoospores few to 50, reniform, laterally biciliate, 5.4 μ wide and 9 μ long, about 10 μ in diameter at encystment, capable of repeated emergence. Oogonia spherical, typically terminal, smooth- and thin-walled, measuring

12.6 to 28.8 μ, average 21.6 μ, in diameter. Antheridia are monoclinous and diclinous, terminal, 1 to 2 per oogonium, clavate, crook-necked, often 8 μ wide and 20 μ long, making narrow contact with the oogonial wall. Oospores aplerotic, single, with a thick, reticulate wall, the oospore completely sheathed with a gelatinous material, germination by the production of a sporangium which subsequently forms a limited number of zoospores.

Parasitic on *Spirogyra insignis* (Hass.) Kütz. and *S. nitida* (Dillw.) Link, Cracow, Poland.

Pythium dictyosporum was first incompletely described from *Spirogyra insignis* (Hass.) Kütz. in 1891; the next year Raciborski presented an illustrated and more detailed account of the fungus, though failing to give a definite diagnosis of the species, this time describing it from *S. nitida* (Dillw.) Link. De Wildeman (1895) contending that the fungus was presented without adequate diagnosis gives a diagnosis based on material cited by Raciborski and his own observations. That de Wildeman is correct in his contention is questionable, as there were specific descriptions published prior to 1895, though these were presented in a rambling and disconnected style. The description above is taken in part from Sparrow (1931a) and from the writer's observations. Sparrow's diagnosis was chosen in preference to de Wildeman's because it is based on more recent and complete observations of the fungus. The writer's studies are based on preserved algal material containing the fungus.

The predominant features of the species are contained in the above diagnosis. Sparrow (1931a) observes that his isolate of *Pythium dictyosporum* produced only diclinous antheridia whereas Raciborski (1892) reports the production of both diclinous and monoclinous; the isolate studied by the writer produced antheridia of both types. The type of antheridium and its mode of application closely resembles that of *P. monospermum;* the sporangia of these two species are likewise similar. The presence of sculptured oospores in the Pythiaceae is confined to two *Pythium* species, whereas in the two remaining families of the order, Albuginaceae and Peronosporaceae, the presence of this type of oospore is not at all uncommon; this point further emphasizes the interrelationship of the families and may be indicative of their phylogeny. *P. dictyosporum* may readily be distinguished from related species in its unique reticulate-walled oospore. The only other member of the genus with a sculptured oospore wall is *P. cystosiphon*, a not closely related species with spherical sporangia.

Pythium dictyosporum has been observed in *Spirogyra* sp. in France by de Wildeman (1895) in the United States by Matthews (1931) and Sparrow (1933), in *S. insignis* and *S. nitida* by Raciborski in Poland, in *S. crassa* Kütz. in the United States by Sparrow (1931a) and in *Vaucheria* sp. by the author. Sparrow states that this species was capable of infecting *Cucumis sativus* L., *Rhizoclonium hieroglyphicum* (Ag.) Kütz. and *Tolypothrix* sp., he

(1932) later reported that *P. dictyosporum* was capable of infecting *Oedogonium* sp. upon inoculation.

10. PYTHIUM TENUE Gobi, Scrip. Bot. Hort. Univ. Imp. Petropol. **15**: 221–226. 1899–1900.

Hyphae fine, isodiametric, branched, measuring 1 to 3 μ in diameter. Sporangia filamentous, similar to the vegetative hyphae, when intramatrical, vesicle exogenous. Zoospores 2 to 60 in a vesicle, reniform, laterally biciliate. Oogonia spherical, smooth, thin-walled, intramatrical, usually acrogenous, measuring 7.2 to 15.6 μ, mostly 9.8 to 12.2 μ, mean 10.3 μ in diameter. Antheridia usually one, occasionally two, per oogonium, more frequently monoclinous than diclinous, antheridial cell clavate, slightly swollen, terminal, not delimited by septum. Oospores single, aplerotic, globose, smooth, thin-walled, measuring 6.0 to 12.1 μ, usually 7.5 to 9.8 μ, mean 8.4 μ in diameter, containing a single reserve globule and a small ellipsoidal refringent body in the protoplasm.

Originally described as parasitic on *Vaucheria sessilis* DC. and *Mesocarpus* sp., Finland.

Pythium tenue is usually restricted to living algal hosts. The observations of the writer are based upon a study of the fungus in living cells of *Vaucheria* sp. collected near Ashland, Missouri. Attempts to culture the organism on agar substrates were unsuccessful; Matthews (1931) encountered the same difficulty.

Though rather free use is made of the undelimited antheridial cell in the segregation of this species from related forms, a septum has been observed in rare instances. The nature of the antheridium, however, is not the sole criterion for specific identification. *P. tenue* may be separated easily from the aplerotic oospore forms such as *P. dissotocum*, *P. gracile* and *P. adhaerens* on the absence of a thickened oospore wall, as well as on its obligate parasitic character. *P. tenue* may be distinguished from *P. angustatum* by the absence of polyandrous oogonia. *P. apleroticum* might be confused with *P. tenue* except that its antheridium is always diclinous and never monoclinous as is common in *P. tenue*. *P. papillatum* is easily distinguished from *P. tenue* by its papillate oogonia, absent in *P. tenue*. The unusually small oogonia of *P. tenue* may likewise assist in the identification of the species.

Gobi points out that *P. entophytum* Pringsh., *sensu* Schenk, does not correspond with Pringsheim's description of the organism. He further identifies *P. tenue* as the fungus that Schenk (1859) confused with *P. entophytum*. Since Zopf transferred *P. entophytum* to the genus *Lagenidium* and Schenk failed to realize the exact identity of his fungus, *P. tenue* Gobi remains the valid nomen.

Pythium tenue has been observed in *Mesocarpus* sp. in Finland by Gobi, in *Spirogyra* sp. in the United States by Matthews (1931), in *Vaucheria* sp. in the United States by the author and Matthews, in *Vaucheria sessilis* DC. in Finland by Gobi and in the United States by Sparrow (1933).

11. PYTHIUM PAPILLATUM Matthews, Jour. Elisha Mitchell Soc. **43**: 229–232. 1932.

Hyphae irregular in size, main filaments measuring up to 24 μ in diameter at base, usually from 2.3 to 10.1 μ, average 7 μ, in diameter, the apex frequently blunt-tipped; numerous bud-like outgrowths in old cultures. Sporangia filamentous, similar to vegetative hyphae, short or long, branched or unbranched; zoospores few to 20 or more, reniform and laterally biciliate, usually 12 μ long and 7.2 μ wide, when encysted about 12 μ in diameter. Oogonia spherical, subspherical, oval, terminal on short branches, intercalary, often catenulate, 1 to 5, measuring 16.8 to 26.4 μ in diameter, thin-walled, smooth or with one or two papillae. Antheridia not produced. Oospores plerotic except for oogonial neck and papillae, single, occasionally two per oogonium, smooth- and moderately thin-walled. Germination not observed.

Isolated from soil in Chapel Hill, N. C., U. S. A.

Pythium papillatum is unique among the species possessing strictly filamentous sporangia in having papillate oogonia and apandrous, plerotic oospores. Though the oogonial papillae of *P. papillatum* may be confused with the subterminal oogonia of *P. monospermum*, the absence of antheridia alone may separate the species.

In addition to the isolation of *Pythium papillatum* from soil in the U. S. A. by Matthews, a culture was obtained by the writer from rotted barley, *Hordeum vulgare* L. roots collected in Missouri, U. S. A.

12. PYTHIUM AFERTILE Kanouse and Humphrey, Papers Mich. Acad. **8**: 129–140. 1927.

Hyphae measuring 3 to 5 μ in diameter, branching, non-septate when young, occasionally septate when old. Sporangia hypha-like, 3 to 5 μ in diameter, 300 μ or more in length, unbranched, quickly collapsing after vesicle formation; zoospores 3 to 30, formed in a terminal, spherical, evanescent vesicle, 9 to 40 μ, average 25 μ, in diameter, the zoospores reniform, laterally biciliate, monoplanetic, measuring 8 to 10 μ in diameter when encysted. Spherical structures resembling chlamydospores are profusely formed, spherical, terminal or intercalary, delimited by septa; by renewed growth forming hyphae or sporangia. Sexual reproduction unknown.

Collected from *Vaucheria* sp. Ann Arbor, Mich., U. S. A.

A culture of this fungus was obtained for study from the Centraalbureau voor Schimmelcultures, Baarn, Holland. The organism received agreed with the description of the species quoted above.

In the absence of a sexual stage it is difficult to identify *Pythium* species. On the basis of the sporangial characters, *Pythium afertile* might be any one of the strictly filamentous species of the genus. Whether the sexual stage will ever be found is doubtful. Its absence may be due to a variety of factors, among them environmental conditions, types of culture media, presence, absence or amount of sex-promoting substances. Although the authors of the species contend that *P. afertile* is a distinct organism, lacking a sexual stage, the disadvantage of giving an organism of this type a binomial can

readily be seen. On the contrary, if a species is to be considered as an entity or a group of like organisms, it is certainly justifiable to describe it and ascribe a binomial to it. If this species is maintained it is understood that *P. monospermum*, *P. adhaerens* and others, lacking sexual development, will automatically become associated with *P. afertile*.

The presence of certain spherical, terminal or intercalary bodies may further distinguish the fungus from allied species. If any significance is to be attached to the presence of chlamydospores, *Pythium afertile* may be considered an ally of *P. perniciosum*. That any degree of significance should be assigned these chlamydospores seems doubtful in the light of our knowledge of the origin and development of oogonia and spherical sporangia which are examined in the discussion following the description of *P. perniciosum*.

P. afertile may either be maintained as a distinct species, lacking a sexual stage, or as a binomial which includes a variety of related species, the sexual stage of which at the time is lacking but which may be encountered upon later observation; transference to another binomial would be mandatory once the sexual stage appeared in a species of the latter category. It seems best to maintain the species pending further study.

Pythium afertile is known from *Gossypium* sp. in the Anglo-Egyptian Sudan by Andrews and Clouston (1938, 1939) and Massey (1936), from *Vaucheria* sp. by Kanouse and Humphrey in the United States and from *Viola tricolor* L. by van Eek (1938) in the Netherlands.

13. Pythium catenulatum Matthews, Studies on the Genus Pythium. 1931.

Hyphae measuring 2 to 4 μ in diameter, branched. Sporangia composed of somewhat inflated hyphae in conjunction with irregularly swollen bud-like lateral outgrowths, forming simple to complex aggregations; zoospores 10 to 20 or more in a vesicle, 6 μ wide by 8 to 11 μ long, reniform and laterally biciliate. Numerous spherical to pyriform asexual reproductive bodies (= conidia, according to Matthews) also present, terminal and intercalary, single or 3 to 8 in a chain, 10 to 20 μ, average 15 μ, in diameter, germinate by production of 1 to 3 germ tubes, never producing sporangia. Oogonia usually spherical, terminal or intercalary, smooth- and thin-walled, measuring 18 to 38 μ in diameter. Antheridia of monoclinous or diclinous origin, from 1 to 12, usually 5 to 6, per oogonium, clavate, crook-necked, making narrow apical contact with the oogonial wall. Oospores plerotic, single, smooth- and thick-walled, containing a single reserve globule and refringent body in the granular protoplasm, oospores measuring 16 to 32 μ in diameter; germination not observed.

Originally described from water containing vegetable debris collected in N. C., U. S. A.

Asexual reproduction in *Pythium catenulatum* is very similar to that found in *P. perniciosum;* there are, however, certain differences, which separate the species. Both species have catenulate spherical, asexual reproductive bodies which germinate only by the production of one to five germ tubes when a suitable environmental condition prevails. In *P. catenulatum*

these spherical bodies range in size from 10 to 20 μ, usually 15 μ, in diameter, the interval between bodies varying from 1 to 35 μ in length; the comparable structures in *P. perniciosum* range in size from 17.3 to 30 μ, usually 24 μ in diameter, with less interval irregularity, usually measuring from 20 to 25 μ between structures. In general habit the asexual reproductive bodies of *P. catenulatum* resemble those of *P. intermedium*, a species lacking filamentous sporangia and a sexual stage. The sporangia of *P. catenulatum* differ from those of *P. perniciosum* in being inflated and having a disjuncted moriform aspect.

The sexual stage of *Pythium catenulatum* is quite like that of *P. arrhenomanes*, both species possessing plerotic oospores and an abundance of functional antheridia. The antheridia of *P. catenulatum* are both monoclinous and diclinous whereas those of *P. arrhenomanes* are strictly diclinous.

The sexual stages of *Pythium perniciosum* and *P. catenulatum* cannot be confused. As stated by Matthews and observed by the writer, *P. perniciosum* possesses aplerotic oospores and one, rarely two, antheridia; *P. catenulatum* possesses plerotic oospores and one to twelve, usually five to six, antheridia. There are no unique or distinguishing macroscopic features evident when *P. catenulatum* is cultivated on sundry nutrient agar substrates, growth being quite like that of *P. debaryanum*, showing copious, loose, aerial, mycelial wefts which are haphazardly disposed.

Pythium catenulatum was originally isolated from water containing plant debris in N. C., U. S. A.; the writer has isolated this species from plant debris collected from the margin of a lake in Mo., U. S. A.

14. Pythium torulosum Coker and Patterson, Jour. Elisha Mitchell Soc. 42: 247–250. 1927.

Hyphae measuring 2.5 to 4 μ in diameter, irregularly branched. Sporangia consisting of few to numerous irregularly branched, inflated toruloid members, forming simple or complex sporangial complexes; zoospores few to 20, 7 to 8 μ in diameter when encysted, reniform and laterally biciliate. Oogonia spherical to subspherical, terminal either on long filaments or short lateral branches, intercalary, measuring 12 to 19 μ, mostly 17 to 18 μ in diameter, smooth- and thin-walled. Antheridia of monoclinous origin, usually from the oogonial stalk, occasionally from the parent filament, usually 1, sometimes 2, per oogonium, borne on a short stalk, rarely branched, antheridial cell not greatly inflated, allantoid-clavate, the apex contacting the oogonial wall. Oospores plerotic, single, with a moderately thin wall.

Isolated from a water culture, *Teleranea nematodes* (Gottsche) Howe and *Thuidium delicatulum* (L.) Mitt., Chapel Hill, N. C., U. S. A.

Though this species is described from Bryophyta, it has been isolated from Phanerogams and proven pathogenic by van Luijk (1934a), Vanterpool (1938), the writer and possibly others.

Various isolates of the fungus exhibit some peculiarities, particularly in the growth habit on agar substrates. The isolates from wheat roots procured

through Vanterpool are typical of the species, although the antheridium usually arises some distance, 25 μ, below the oogonium on the oogonial stalk, whereas Coker and Patterson figure the antheridium arising in close proximity, 5 to 10 μ, to the oogonium. Such a difference cannot be deemed sufficient to separate Vanterpool's strain from the type species. Van Luijk's strain from grass roots conforms more closely to the delineations of the species than Vanterpool's in that the antheridium arises in close proximity to the oogonium on the oogonial stalk. A culture from barley isolated by the writer is typical of the species and agrees with van Luijk's fungus. A fungus described by Petri (1930) as being a member of the *Pythium gracile* group is in all probability *P. torulosum;* this has also been suggested by Vanterpool (1938).

There are certain macroscopic differences in the mycelial habit of isolates of this fungus. Vanterpool reports that his strain produces a vigorous mycelial growth with a tendency toward aerial development. Van Luijk's strain grows less vigorously and exhibits a very definite rosette habit on solid substrates with only meagre aerial development. The writer's strain shows a definite tendency toward a radiate habit and only a slight tendency toward rosetting. Vanterpool separates his strain from van Luijk's on the basis of the growth habit and position of the antheridium, but retains both in the species. The writer's experience has shown that too much emphasis should not be placed on the exact nature of the growth habit of *Pythium* spp., that some variation is often observed in forms morphologically indistinguishable. This is particularly well exemplified in *P. vexans.*

The asexual stage of *Pythium torulosum* is more or less typical of all the species possessing lobulate sporangia. *P. torulosum* may be distinguished readily from *P. graminicolum*, to which it is closely allied, by the morphology of the antheridial cell. In *P. torulosum* there is usually only one antheridium, rarely two, which is only slightly inflated and is typically allantoid-clavate, usually sessile but sometimes borne on a short antheridial stalk. The antheridia of *P. graminicolum* are more numerous and are inflated, crook-necked, clavate, borne on a longer antheridial stalk, rarely sessile. There is also a difference in the size of the oogonia of the two species: 12.0 to 19.0 μ in diameter in *P. torulosum* compared with 16.5 to 28.6 μ in diameter according to Subramaniam (1928), often larger, 24 to 36 μ in diameter. *P. torulosum* is easily separated from other plerotic oospore species with inflated filamentous sporangia, *P. inflatum*, *P. arrhenomanes*, and *P. periilum*, in possessing monoclinous antheridia.

The temperature-growth response of *P. torulosum* may conveniently be used as an adjunct to specific identification.

Originally described from water, *Teleranea nematodes* (Gottsche) Howe and *Thuidium delicatulum* (L.) Mitt. by Coker and Patterson, Matthews (1931) later reports *Pythium torulosum* again from water and ". . . a collection of leafy liverworts and mosses . . . ," further stating that Coker and Patterson obtained this fungus from *Trichocolea tomentella* (Ehr.) Dum., all

from N. C., U. S. A.; the writer obtained an isolate of the fungus from rotted roots of *Hordeum vulgare* L. in Mo., U. S. A. Van Luijk (1934) records *P. torulosum* from *Agrostis stolonifera* L. and *Festuca duriuscula* L. from the Netherlands and Vanterpool (1938) from *Triticum aestivum* L. roots in England. The fungus reported by Petri (1930) from wheat in Italy may possibly be *P. torulosum*. Ten Houten (1939) reports what is believed to be this species from *Abies grandis* Lindl. and *Pinus sylvestris* L. in the Netherlands.

15. PYTHIUM GRAMINICOLUM Subramaniam. Agr. Res. Inst. Pusa (India). Bull. 177: 1–7. 1928.

Hyphae measuring 3 to 7 μ in diameter, irregularly branched, hyaline and granular. Sporangia inflated filamentous, simple or irregularly branched, usually forming irregular toruloid, digitate complexes, terminal or intercalary; zoospores 15 to 48 in number, 8 to 11 μ in diameter when encysted, reniform and laterally biciliate, capable of repeated emergence. Oogonia spherical, smooth and thin walled, terminal, intercalary, measuring 16.5 to 36.2 μ, mean 25.0 μ, in diameter. Antheridia are of monoclinous origin, borne on stalks of varied length, 1 to 6 in number, the antheridial cell clavate with flattened apex. Oospores plerotic, single, smooth- and moderately thick-walled, hyaline or somewhat brownish, 15.4 to 35.3 μ, mean 23.0 μ, in diameter; germination not observed.

Originally described from *Triticum aestivum* L., India.

Since Subramaniam presented the description of *Pythium graminicolum* considerable controversy has arisen as to the exact identity of certain root-infesting *Pythium* spp. possessing an inflated filamentous asexual stage. Several years following Subramaniam's presentation, Drechsler (1936) partially resolved the problem in a treatise on *P. graminicolum* and *P. arrhenomanes*. Prior to this, the two species were considered synonymous by some students of the genus.

Type cultures of *Pythium graminicolum* are not available. The writer was fortunate in receiving from Subramaniam a number of cultures isolated from sugarcane; a brief report concerning the occurrence of this organism on sugarcane has been published (Subramaniam 1936a). A study of the sugarcane isolates revealed them to be identical with the description of the species.

The antheridia are monoclinous either from the oogonial stalk or its parent filament and originate in moderate proximity to the oogonium, usually not over 60 μ below it. The number of antheridia varies from 1 to 6 per oogonium. Usually the antheridia originate on separate stalks, but occasionally the stalk may be branched, bearing two antheridial cells. In two instances sessile antheridia were observed; Subramaniam gives illustrations showing this condition in his original work on the species. The antheridial cell is usually curved, clavate and bluntly tipped, making apical contact with the oogonial wall. The antheridia, because of their origin, are not radially arranged about the oogonium; this is a distinguishing factor in the separation of *P. graminicolum* from *P. arrhenomanes*. Drechsler reports similar observations concerning the antheridia.

The oogonia of *Pythium graminicolum* are invariably acrogenous, spherical, smooth and thin-walled and range in size from 16.5 to 36.2 μ, mean 24.8 μ, in diameter. Oospores are plerotic, smooth and thick-walled, ranging in size from 15.4 to 35.3 μ, mean 23.7 μ, in diameter. For convenience, a comparison of data on the size of sexual reproductive bodies is tabulated below:

Author	*Host*	*Oogonia* (μ)	*Oospores* (μ)
Subramaniam (1928)	Wheat	16.5–28.6	15.4–26.4
Subramaniam (1936)	Sugarcane	16.9–33.0 av. 25.0	16.3–30.8 av. 23.0
Rands and Dopp (1938)	Sugarcane	19.0–28.0 m. 23.0	———
Matthews (1931)	Sarracenia	24.0–36.0 av. 30.0	21.6–32.0 av. 28.0
Writer	Sugarcane	16.5–36.2 m. 24.8	15.4–35.3 m. 23.7
Writer	Barley	18.7–29.3 m. 24.1	18.0–29.9 m. 23.2
Writer	Wheat	17.3–31.2 m. 25.1	16.1–30.0 m. 24.0
Writer	Corn	17.1–30.8 m. 24.9	18.8–29.8 m. 23.3

Only one isolate each of a series from a given host is presented from the writer's collection. Those listed are considered typical of the series. Occasionally in old cultures spherical bodies are observed which resemble oogonia. Under suitable environmental conditions these structures germinate by the production of a germ tube; production of zoospores has not been observed. The term conidia has been used for these structures. Inasmuch as they are found singly and are not deciduous, application of this term would seem unfortunate. The structures appear to be analogous to those found in *Pythium ultimum* in which species they have been demonstrated to be unfertilized oogonia apparently functioning as food reservoirs.

Carpenter (1921) first ascribed the binomial *Pythium butleri* to the Hawaiian sugarcane root parasite. Seven years later (1928b) he referred the fungus to *P. aphanidermatum* and then later (1934) identified the organism as *P. graminicolum*, considering *P. arrhenomanes* synonymous with *P. graminicolum*. Drechsler in 1936 assigned the binomial *P. arrhenomanes* to the sugarcane parasite, referring Carpenter's fungus to this species; Rands and Dopp (1938b) concur with him in this.

A study of four isolates of a Hawaiian sugarcane fungus received from Carpenter were identified by the writer as *Pythium graminicolum*. If the cultures received are typical of the sugarcane series, this fungus is incorrectly transferred to *Pythium arrhenomanes* and it should be maintained under the binomial *P. graminicolum*.

Following Drechsler's scheme (1936), with which the writer is in agreement, *Pythium graminicolum* may be distinguished from *P. arrhenomanes*, its closest ally, on the basis of antheridial habit and certain cultural peculiarities. In *P. graminicolum* the antheridia are monoclinous, arising in rather close proximity, within 60 μ, to the oogonium, antheridial cells few,

1 to 6, usually 2 to 4, and irregularly arranged about the oogonium. In *P. arrhenomanes*, on the other hand, the antheridia are diclinous and have no discernible connection with the oogonial stalk, the antheridial cells numerous, 1 to 25, usually in excess of 8, and fairly regularly arranged about the oogonium. *P. graminicolum* usually fruits in culture in moderate abundance on ordinary culture media, the antheridia and oogonia retaining their identity many weeks after fecundation has occurred; *P. arrhenomanes* fruits sparingly on ordinary culture media, the antheridia and oogonia losing their identity soon after fecundation has taken place.

Macroscopically and in their temperature-growth relations, *P. graminicolum* and *P. arrhenomanes* are indistinguishable.

Ho, Meredith, and Melhus (1941) have preferred to use the binomial *Pythium graminicola* instead of the binomial *P. graminicolum* originally established by Subramaniam. Subramaniam apparently took the liberty of turning the indeclinable noun, graminicola, into an adjective agreeing with the genus name, and since this is the original usage, it is the form which the writer retains.

Hosts for *Pythium graminicolum* are cited in the following table:

PLANTS REPORTED BY VARIOUS INVESTIGATORS AS SUSCEPTIBLE TO PYTHIUM GRAMINICOLUM

Agropyron cristatum (L.) Gaertn. UNITED STATES: Buchholtz (1942b).
Ananas comosus Merr. HAWAII: Parris (1940).
Avena sativa L. INDIA: Subramaniam (1936). UNITED STATES: Ho and Melhus (1938); Author.
Curcuma longa L. CEYLON: Anonymous (1936a).
Gossypium sp. ANGLO-EGYPTIAN SUDAN: Massey (1936).
Hordeum vulgare L. INDIA: Subramaniam (1936). UNITED STATES: Ho and Melhus (1938); Ho, Meredith, Melhus (1941); Author.
Oryza sativa L. HAWAII: Parris (1940).
Panicum miliaceum L. UNITED STATES: Ho and Melhus (1938).
Phleum pratense L. UNITED STATES: Ho and Melhus (1938).
Pisum arvense L. UNITED STATES: Weimer (1940).
Saccharum officinarum L. HAWAII: Carpenter (1934); Lyon (1936); Martin (1941); Martin and Carpenter (1935); Parris (1940). INDIA: Subramaniam (1936). MAURITIUS: Shepherd (1933). PHILIPPINE IS.: Ocfemia (1939). PUERTO RICO: Seaver *et al.* (1932). UNITED STATES: Rands (1930); Rands and Abbott (1939); Rands and Dopp (1934, 1938a, 1938b); Stevenson and Rands (1938).
Secale cereale L. UNITED STATES: Ho and Melhus (1938).
Setaria glauca Beauv. UNITED STATES: Ho, Meredith and Melhus (1941).
Soil. UNITED STATES: Matthews (1931); Meredith (1938).
Sorghum vulgare Pers. INDIA: Subramaniam (1936a). ITALY: Goidanich (1939). UNITED STATES: Ho, Meredith and Melhus (1941); Author.
S. vulgare var. *sudanense* (Piper) Hitchc. HAWAII: Lyon (1936).
Triticum aestivum L. INDIA: Subramaniam (1928, 1936a); Butler and Bisby (1931). CANADA: Vanterpool (1938); Vanterpool and Truscott (1932). ENGLAND: Vanterpool (1938). UNITED STATES: Ho and Melhus (1938, 1940); Ho, Meredith and Melhus (1941); Author.
Vicia sp. UNITED STATES: Weimer (1940).
Zea mays L. INDIA: Subramaniam (1936a). MALAYA: Milsum and Grist (1941). UNITED STATES: Buchanan (1938); Ho (1941); Ho and Koepper (1942); Ho and Melhus (1938, 1940); Melhus (1940); Melhus *et al.* (1939, 1940); Author.
Zingiber officinale Roscoe. CEYLON: Anonymous (1936a); Park (1935).

16. PYTHIUM INFLATUM Matthews, Studies on the Genus Pythium. 1931.

Hyphae well developed on corn meal agar, narrow, measuring 1 to 4 μ in diameter. Sporangia irregular to spherical toruloid outgrowths which measure 8 to 20 μ in diameter; zoospores unknown. Oogonia rarely found, spherical and smooth, acrogenous or intercalary, measuring 18 to 26 μ in diameter. Antheridia of diclinous origin, 1 to 2 per oogonium. Oospores plerotic, single, with a thick wall, containing a reserve globule and a refringent body embedded in the granular protoplasm.

Isolated from a decaying seedling in a culture dish of *Vaucheria*, Chapel Hill, N. C., U. S. A.

Because material of this fungus was unavailable to the writer, discussion of the species must be confined to the diagnosis presented by Matthews and the remarks made in the original article by her.

Morphologically, *Pythium inflatum* exhibits affinities to *P. torulosum*, *P. graminicolum*, *P. arrhenomanes*, and *P. periilum*. Matthews states, "This plant is similar to *P. monospermum* but differs from it in the larger toruloid outgrowths on the mycelium." Since the sporangia of *P. inflatum* and *P. monospermum* are not comparable, it seems advisable to compare *P. inflatum* with the more closely related forms. The antheridia of *P. torulosum* and *P. graminicolum* are monoclinous, origin not proximal to the oogonium. Matthews separates *P. inflatum* from *P. graminicolum* in noting ". . . the smaller hyphae, the absence of large spherical conidia, slowness of growth, absence of zoospores, rareness of oogonia and the type and number of of antheridia." The antheridial character is sufficient for specific segregation in this case. *P. arrhenomanes* and *P. periilum*, like *P. inflatum*, have diclinous antheridia. The antheridial cells arise from separate branches in both *P. arrhenomanes* and *P. inflatum*. Whereas in *P. arrhenomanes* the antheridial branches are frequently divided and the antheridial cells are many, up to 25 per oogonium, in *P. inflatum* the antheridial branches are simple and the antheridial cells few, one to two per oogonium. *P. periilum*, though possessing diclinous antheridia, is distinctly different from *P. inflatum* in having the antheridial cells arising from a single antheridial branch.

The oogonia and oospores are similar in *Pythium inflatum*, *P. torulosum*, *P. graminicolum*, *P. arrhenomanes*, and *P. periilum*.

Pythium inflatum is not known from any substrate other than the vegetable debris from which it was originally described.

17. PYTHIUM ARRHENOMANES Drechsler, Phytopathology **18**: 873–875. 1928.

Nematosporangium arrhenomanes (Drechs.) Sideris, Mycologia **23**: 252–295. 1931.
N. arrhenomanes var. *hawaiianensis* Sideris l.c.
N. epiphanosporon Sideris l.c.
N. hyphalosticton Sideris l.c.
N. leiohyphon Sideris l.c.
N. leucosticton Sideris l.c.
N. polyandron Sideris l.c.
N. rhizophthoron Sideris l.c.

N. spaniogamon Sideris l.c.
N. thysanohyphalon Sideris l.c.
Pythium arrhenomanes var. *canadensis* Vanterpool & Truscott, Canad. Jour. Res. **6**: 68–93. 1932.
Pythium arrhenomanes var. *philippinensis* Roldan, Philipp. Agr. **21**: 165–176. 1932.

Mycelium intra- and intercellular, hyphae measuring 2.0 to 5.5 μ in diameter. Sporangia inflated, filamentous, lobulate, forming complexes of elements up to 20 μ or more in diameter, zoospores 20 to 50 or more in a vesicle borne on an evacuation tube usually 3 to 4 μ in diameter and of variable length, up to 75 μ, biciliate, measuring approximately 12 μ in diameter upon encystment. Oogonia subspherical to spherical, acrogenous, occasionally intercalary, smooth- and thin-walled, measuring 17.3 to 56.3 μ, mean 30.1 μ, in diameter. Antheridia of diclinous origin, numerous, 15 to 25 often visible, usually borne terminally though occasionally laterally on 4 to 8 branches each usually contributing up to 4 antheridia, antheridial cells are crook-necked, 6 to 9 μ wide and 12 to 25 μ long, making narrow contact with the oogonium. Oospores plerotic, 15.5 to 54.2 μ, mean 28.2 μ, in diameter, wall 1.2 to 2.0 μ, usually 1.6 μ thick, containing a single reserve globule.

Originally described from *Zea mays* L. roots in Wisconsin, U. S. A.

The diagnosis given concerns the identity of the *Pythium* sp. that Johann, Holbert and Dickson (1926, 1928) report as the cause of a seedling disease of dent corn.

Rands and Dopp (1934) have published the most extensive study of *Pythium arrhenomanes;* a subsequent paper by these authors (1938b) deals with this and associated species.

Sideris (1931) in his study of *Nematosporangium* spp. (*Pythium* spp.) lists and described eight new species and three new varieties. Rands and Dopp (1934) have since combined these organisms in the binomial *P. arrhenomanes*. A study of Sideris' fungi and a series of isolates of *P. arrhenomanes*, including the varieties *P. arrhenomanes canadensis*, *P. arrhenomanes hawaiiensis* and *P. arrhenomanes philippinensis* was undertaken by the writer.

The various isolates of *Pythium arrhenomanes*, including those of Sideris, were observed on a series of nutrient substrates. The morphology of the organisms was noted in each case and measurements of the oogonia made. Oospore measurements were not taken because the oospores are plerotic, less abundant than oogonia and frequently aborted. Oogonial measurements of representatives of each series are presented:

Organism	*Host*	*Range* (μ)	*Mean* (μ)
P. arrhenomanes	Sugarcane	28.6–37.3	33.1
Do.	Do.	17.3–29.1	23.5
Do.	Do.	28.0–43.6	34.7
Do.	Do.	26.3–44.2	33.2
Do.	Do.	19.0–31.0	24.2
Do.	Do.	32.1–56.3	42.0
Do.	Corn	25.1–36.8	30.1
Do.	Do.	31.0–50.1	39.0
Do.	Do.	18.3–28.7	23.1
P. arrhenomanes canadensis	Wheat	27.7–44.6	34.9

Organism	*Host*	*Range* (μ)	*Mean* (μ)
P. arrhenomanes hawaiianensis	Pineapple	23.0–37.4	30.3
P. arrhenomanes philippinensis	Corn	22.1–39.4	30.1
P. spaniogamon	Pineapple	23.0–34.6	30.2
P. hyphalosticton	Do.	30.0–46.3	36.1
P. polyandron	Do.	26.5–47.0	38.4
P. thysanohyphalon	Do.	27.1–48.1	35.8
P. rhizophthoron	Do.	26.3–38.0	30.8
P. leucosticton	Bilbergia	27.8–49.0	36.4
P. leiohyphon	Pineapple	29.1–52.0	37.5
P. epiphanosporon	Do.	23.8–48.3	34.3

The antheridia of each isolate studied were identical in that the antheridial stalks were diclinous with no demonstrable connection with the oogonial stalk. Each antheridial stalk bore one, occasionally two, narrow, clavate and crook-necked antheridial cell which in the aggregate varies in number from one to twenty-five; these were apically applied to the oogonial wall and were more or less radiately arranged about the oogonium, with an approximately equal interval between cells.

Though individual differences may be noted in the oogonial size of certain isolates, there exist a sufficient number of intermediate or overlapping groups to integrate the series into a single natural unit. The uniform antheridial character, despite the variation in numbers, is additional evidence that the organisms listed above represent a single, natural group. Those listed as other than *Pythium arrhenomanes* must be considered synonymous with *P. arrhenomanes;* their similarity in growth habit and temperature-growth relations is presented to further attest to their synonymity.

The observations of the writer corroborate the investigation of Rands and Dopp.

Pythium arrhenomanes differs from *P. inflatum* in possessing antheridial branches which are frequently divided and in having many antheridial cells, up to twenty-five, usually more than ten, per oogonium. The antheridial stalks are simple and the antheridial cells few, one to two per oogonium, in *P. inflatum*. *P. periilum* is readily separated from *P. arrhenomanes* in having the two to five antheridial cells originating from a single antheridial stalk that is characteristically adnate to the oogonium. The distinction between *P. arrhenomanes* and *P. graminicolum* is discussed under *P. graminicolum*.

Pythium arrhenomanes is reported from the hosts listed below:

Aegilops triuncialis L. UNITED STATES: Fischer *et al.* (1942); Vanterpool and Sprague (1942).
Agropyron amurense Drob. UNITED STATES: Fischer *et al.* (1942) Vanterpool and Sprague (1942).
A. caninum (L.) Beauv. UNITED STATES: Vanterpool and Sprague (1942).
A. ciliare (Trin.) Franch. UNITED STATES: Fischer *et al.* (1942); Vanterpool and Sprague (1942).
A. cristatum (L.) Gaertn. CANADA: Bisby *et al.* (1938); Conners (1935); Vanterpool (1940b). UNITED STATES: Fischer *et al.* (1942); Sprague and Atkinson (1942); Vanterpool and Sprague (1942).
A. dasystachyum (Fisch.) Scribn. UNITED STATES: Fischer *et al.* (1942); Vanterpool and Sprague (1942).

A. desertorum (Fisch.) Schult. UNITED STATES: Fischer *et al.* (1942); Vanterpool and Sprague (1942).
A. elongatum (Host) Beauv. UNITED STATES: Fischer *et al.* (1942).
A. inerme (Scribn. and Sm.) Rydb. UNITED STATES: Sprague.
A. intermedium (Host) Beauv. UNITED STATES: Fischer *et al.* (1942): Vanterpool and Sprague (1942).
A. michnoi Roshev. UNITED STATES: Sprague.
A. pauciflorum Hitchc. CANADA: Vanterpool (1940b).
A. pungens (Pers.) Roem. and Schult. UNITED STATES: Vanterpool and Sprague (1942).
A. repens (L.) Beauv. CANADA: Bisby *et al.* (1938); Conners (1935); Vanterpool (1940b). UNITED STATES: Fischer *et al.* (1942); Sprague and Atkinson (1942); Vanterpool and Sprague (1942).
A. riparium Scribn. and Sm. UNITED STATES: Fischer *et al.* (1942); Vanterpool and Sprague (1942).
A. sibiricum (Willd.) Beauv. UNITED STATES: Fischer *et al.* (1942).
A. smithii Rydb. CANADA: Vanterpool. UNITED STATES: Sprague.
A. spicatum (Pursh) Scribn. UNITED STATES: Fischer *et al.* (1942); Vanterpool and Sprague (1942).
A. tenerum Vasey. CANADA: Bisby *et al.* (1938); Conners (1935).
A. trachycaulum (Link) Malte. UNITED STATES: Fischer *et al.* (1942); Vanterpool and Sprague (1942).
A. trichophorum (Link) Richt. UNITED STATES: Fischer *et al.* (1942); Vanterpool and Sprague (1942).
A. ugamicum Drobov. UNITED STATES: Sprague.
Ammophila arenaria (L.) Link. UNITED STATES: Fischer *et al.* (1942); Vanterpool and Sprague (1942).
Ananas comosus Merr. HAWAII: Johnson (1935); Parris (1940); Sideris (1931).
Andropogon furcatus Muhl. UNITED STATES: Fischer *et al.* (1942).
Arrhenatherum elatius (L.) Mert. and Koch. UNITED STATES: Fischer *et al.* (1942); Vanterpool and Sprague (1942).
Avena fatua L. CANADA: Bisby *et al.* (1938); Conners (1935); Vanterpool (1940b). UNITED STATES: Fischer *et al.* (1942); Vanterpool and Sprague (1942).
A. sativa L. CANADA: Bisby *et al.* (1938); Conners (1935); Vanterpool and Truscott (1932). UNITED STATES: Sprague and Atkinson (1942); Vanterpool and Sprague (1942); Author.
Bilbergia sp. HAWAII: Parris (1940); Sideris (1931).
Bouteloua curtipendula (Michx.) Torr. UNITED STATES: Fischer *et al.* (1942); Vanterpool and Sprague (1942).
B. gracilis (H.B.K.) Lag. UNITED STATES: Fischer *et al.* (1942); Vanterpool and Sprague (1942).
Brachypodium sylvaticum (Huds.) Beauv. UNITED STATES: Fischer *et al.* (1942); Vanterpool and Sprague (1942).
Bromus carinatus Hook and Arn. UNITED STATES: Vanterpool and Sprague (1942).
B. erectus Huds. UNITED STATES: Fischer *et al.* (1942); Vanterpool and Sprague (1942).
B. inermis Leyss. CANADA: Bisby *et al.* (1938); Conners (1935); Vanterpool (1940b). UNITED STATES: Fischer *et al.* (1942); Sprague and Atkinson (1942); Vanterpool and Sprague (1942).
B. marginatus Nees. UNITED STATES: Fischer *et al.* (1942).
Cajanus cajan Millsp. HAWAII: Parris (1940); Sideris (1931).
Chaetochloa viridis Scribn. CANADA: Conners (1935).
Commelina nudiflora L. HAWAII: Parris (1940); Sideris (1931).
Echinochloa crus-galli (L.) Beauv. UNITED STATES: Fischer *et al.* (1942); Vanterpool and Sprague (1942).
Elymus canadensis L. UNITED STATES: Sprague.
E. condensatus Presl. UNITED STATES: Sprague.
E. giganteus Vahl. UNITED STATES: Sprague.
E. glaucus Buckl. UNITED STATES: Fischer *et al.* (1942); Vanterpool and Sprague (1942).
E. interruptus Buckl. UNITED STATES: Fischer *et al.* (1942); Vanterpool and Sprague (1942).
E. junceus Fisch. UNITED STATES: Fischer *et al.* (1942); Sprague and Atkinson (1942); Vanterpool and Sprague (1942).

E. macounii Vasey. UNITED STATES: Fischer *et al.* (1942).
E. sibiricus L. UNITED STATES: Sprague.
Festuca elatior L. UNITED STATES: Fischer *et al.* (1942).
F. elatior var. *arundinacea* (Screb.) Wimm. UNITED STATES: Fischer *et al.* (1942).
F. octoflora Walt. UNITED STATES: Sprague.
F. rubra L. var. *commutata* Gaud. UNITED STATES: Vanterpool and Sprague (1942).
Hordeum distichon L. UNITED STATES: Sprague.
H. jubatum L. UNITED STATES: Fischer *et al.* (1942).
H. vulgare L. CANADA: Bisby *et al.* (1938); Vanterpool and Truscott (1932). UNITED STATES: Vanterpool and Sprague (1942); Wood and Nance (1938); Author.
Ipomoea batatas Lam. HAWAII: Parris (1940); Sideris (1931).
Muhlenbergia racemosa (Michx.) B.S.P. UNITED STATES: Fischer *et al.* (1942).
Musa cavendishii Lamb. HAWAII: Parris (1940); Sideris (1931).
Oryzopsis hymenoides (Roem. and Schult.) Rick. UNITED STATES: Fischer *et al.* (1942); Sprague and Atkinson (1942).
Panicum barbinode Trin. HAWAII: Sideris (1931).
P. capillare L. UNITED STATES: Sprague.
P. miliaceum L. UNITED STATES: Fischer *et al.* (1942); Sprague and Atkinson (1942); Vanterpool and Sprague (1942).
P. subvillosum Ashe. UNITED STATES: Sprague.
P. virgatum L. UNITED STATES: Sprague and Atkinson (1942).
Phalaris arundinacea L. CANADA: Bisby *et al.* (1938); Conners (1935); Vanterpool (1940b).
Phaseolus aureus Roxb. HAWAII: Parris (1940); Sideris (1931).
Phleum pratense L. CANADA: Bisby *et al.* (1938); Conners (1935); Vanterpool (1940b). UNITED STATES: Sprague and Atkinson (1942).
Saccharum barberi Jesweit. UNITED STATES: Rands and Dopp (1938b).
S. officinarum L. HAWAII: Martin (1942); Parris (1940); Sideris (1931); Stevenson and Rands (1938). MAURITIUS: Stevenson and Rands (1938); Wiehe (1940a, b). PHILIPPINE ISLANDS: Roldan (1932). UNITED STATES: Brandes, Dowell and Baker (1936); Edson and Wood (1936); Flor (1930a, 1930b); Rands (1930); Rands and Abbott (1937, 1939); Rands, Abbott and Summers (1936); Rands and Dopp (1934, 1938a, 1938b); Stevenson and Rands (1938); Tims (1932b); Wood and Nance (1938).
S. robustum Jesweit. UNITED STATES: Rands and Dopp (1938b).
S. sinense Roxb. UNITED STATES: Rands and Dopp (1938b).
S. spontaneum L. UNITED STATES: Rands and Dopp (1938b).
Schedonnardus paniculatus (Nutt.) Trel. UNITED STATES: Sprague.
Secale cereale L. CANADA: Bisby *et al.* (1938); Vanterpool and Truscott (1932). UNITED STATES: Sprague and Atkinson (1942); Vanterpool and Sprague (1942); Author.
Setaria italica (L.) Beauv. UNITED STATES: Fischer *et al.* (1942); Sprague and Atkinson (1942); Vanterpool and Sprague (1942).
S. lutescens (Weigel) F. T. Hubb. UNITED STATES: Sprague.
S. viridis (L.) Beauv. UNITED STATES: Fischer *et al.* (1942); Vanterpool and Sprague (1942). CANADA: Bisby *et al.* (1938); Vanterpool (1940b).
Solanum tuberosum L. HAWAII: Parris (1940); Sideris (1931).
Sorghastrum nutans (L.) Nash. UNITED STATES: Fischer *et al.* (1942); Vanterpool and Sprague (1942).
Sorghum sp. UNITED STATES: Altstatt (1942); Brown (1940). CANADA: Vanterpool (1940).
S. vulgare Pers. ITALY: Goidanich (1939). UNITED STATES: Bowman *et al.* (1937); Brown (1940); Cushing *et al.* (1940); Edson and Wood (1937); Elliott *et al.* (1936, 1937); Ezekiel (1938); Fischer *et al.* (1942); Jackson (1938); Johnston (1942); Jones and Gaines (1938); Kendrick and Briggs (1939); Melchers (1940); Middleton (1938); Myers (1934); Nance (1939, 1940); Sprague and Atkinson (1942); Vanterpool and Sprague (1942); Wagner (1936).
S. vulgare var. *sudanense* (Piper) Hitchc. UNITED STATES: Fischer *et al.* (1942); Sprague and Atkinson (1942); Vanterpool and Sprague (1942); Author.
Sphenopholis obtusata (Michx.) Scribn. UNITED STATES: Sprague.
Stipa comata Trin. UNITED STATES: Fischer *et al.* (1942); Vanterpool and Sprague (1942).
S. spartea Trin. UNITED STATES: Fischer *et al.* (1942).

S. viridula Trin. UNITED STATES: Sprague and Atkinson (1942).
Triticum aestivum L. CANADA: Bisby *et al.* (1938); Conners (1935); Garrett (1934); Graham and Greenberg (1939); Simmonds (1939a); Vanterpool and Truscott (1932). ENGLAND: Vanterpool (1938). HAWAII: Parris (1940); Sideris (1931). UNITED STATES: Maneval (1940); Sprague and Atkinson (1942); Vanterpool and Sprague (1942); Author.
T. dicoccum Schrank. UNITED STATES: Sprague and Atkinson (1942); Vanterpool and Sprague (1942).
T. durum Dest. UNITED STATES: Sprague and Atkinson (1942); Vanterpool and Sprague (1942).
Uniola latifolia Mich. UNITED STATES: Author.
Vicia faba L. HAWAII: Parris (1940); Sideris (1931).
Zea mays L. CANADA: Bisby *et al.* (1938); Vanterpool and Truscott (1932). HAWAII: Parris (1940); Sideris (1931). PHILIPPINE ISLANDS: Roldan (1932). UNITED STATES: Branstetter (1927); Drechsler (1928); Johann, Holbert and Dickson (1926, 1928); Koehler and Holbert (1930); Maneval (1937); Mumford (1930); Mumford and Shirkey (1937); Rands and Dopp (1934, 1938a, 1938b); Sprague and Atkinson (1942); Valleau, Karraker and Johnson (1926); Vanterpool and Sprague (1942); Author.

18. PYTHIUM PERILUM Drechsler, Jour. Wash. Acad. **20**: 398–418. 1930.

Hyphae measuring 1.5 to 6 μ, usually 3.5 to 6 μ, in diameter. Appressoria acrogenous, knob-like, often 7 μ wide and 7 to 10 μ long. Sporangia composed of both undifferentiated and inflated, dactyloid mycelial elements, measuring up to 12 μ in diameter, forming relatively simple aggregates; zoospores up to 75 in number formed in a vesicle borne on an evacuation tube up to 0.5 mm. in length and 3 to 4 μ wide, reniform, laterally bicilliate, 8 to 9 μ in diameter at encystment, capable of repeated emergence. Oogonia subspherical, smooth- and thin-walled, acrogenous or intercalary, the oogonium often including a portion of the supporting filament, up to 4 μ in length, oogonia measuring 16 to 22 μ, average 18.8 μ, in diameter. Antheridia diclinous, infrequently from the oogonial stalk some distance from the oogonium, varying from 2 to 5 in number, acrogenous or infrequently lateral, all on branching prolongations of a single hypha, usually including several similar vegetative prolongations wrapped about the oogonium and oogonial stalk, the antheridial cells crook-necked, 4 to 5 μ wide and 7 to 14 μ long, the bluntly rounded apex making narrow oogonial contact. Oospores plerotic, single, 14 to 20 μ, average 17.3 μ, in diameter, with a wall 1.1 to 1.8 μ, average 1.5 μ thick, containing a single reserve globule and an oblate ellipsoidal or subspherical refringent body.

Isolated from roots of *Saccharum officinarum* L., Louisiana, U. S. A.

A more complete understanding of the species may be afforded by a discussion of the interrelationships of this species and allied forms.

Drechsler recently (1940) elaborated upon the original diagnosis but did not present any remarks concerning the systematic position of the fungus. Stevenson and Rands (1938) present an abbreviated description of the fungus in their discussion of the fungi and bacteria associated with sugarcane and its products.

Observations made from a study of the type culture indicate that on the basis of its sporangial habit this species is intermediate between *Pythium monospermum* and *P. myriotylum*. In the former the sporangial elements appear as entirely undifferentiated vegetative elements, whereas in the latter the sporangia may consist of outwardly undifferentiated filaments, but more

often include swollen, dactyloid elements which may or may not be arranged in complex units. *P. periilum* differs considerably however, from *P. monospermum* and *P. myriotylum* in its sexual phase. A plerotic oospore is common to both *P. periilum* and *P. monospermum*, while *P. myriotylum* possesses aplerotic oospores. The antheridial cells of *P. monospermum* arise from separate antheridial branches while those of *P. periilum* arise from a single antheridial branch. The antheridial habit of *P. periilum* resembles that of *P. adhaerens*, previously discussed. In *P. adhaerens* the antheridial branch is not closely associated with the oogonium, always remaining distinctly discernible and lacking vegetative prolongations. The antheridial stalk of *P. periilum* is usually intimately associated with the oogonium, applying itself to the oogonial wall and frequently encircling the oogonium. Considerable difficulty is often encountered in tracing the origin of the individual antheridial cells because of the application of the parent filament and the frequent presence of vegetative prolongations comparable to the individual antheridial stalks but lacking the acrogenous antheridium.

The antheridial habit of *Pythium periilum* is sufficient to distinguish it from its congeners.

Pythium periilum has been reported from roots of sugarcane, *Saccharum officinarum* L., by Drechsler (1930a, 1940), Rands (1930), Rands and Dopp (1938b), Stevenson and Rands (1938), and from *Agropyron repens* (L.) Beauv. by Fischer *et al.* (1942) in the United States.

19. Pythium indigoferae Butler, Mem. Dept. Agr. India Bot. 1^5: 1–160. 1907.

Nematosporangium indigoferae (Butler) Sideris, Mycologia **23**: 252–295. 1931.

Hyphae very irregular in size, measuring up to 8 μ in diameter, frequently forming large lateral, spherical to cylindrical outgrowths up to 12 μ in diameter, similar to sporangia. Sporangia inflated filamentous, usually sparingly formed, composed of swollen digitate simple or branched elements which may form simple or complex aggregations; zoospores 4 to 20. Oogonia spherical, acrogenous on short lateral branches or borne laterally or tangentially in the sporangial complexes, measuring 18 to 20 μ in diameter. Antheridia monoclinous, occasionally diclinous, single, usually arising in close proximity to the oogonium, antheridial cell more or less allantoid, clavate, the antheridial stalk and cell nearly straight, the oogonial stalk and oogonium strongly curved toward the antheridium. Oospore aplerotic, single moderately thick-walled, oospores measuring 13 to 18 μ in diameter; germination prompt by the production of a hypha.

Epiphytic on leaves of *Indigofera arrecta* Hochst., Calcutta, India.

The diagnosis given for *Pythium indigoferae* is taken from the original work of Butler (1907). This fungus has a peculiar habitat, namely in the waxy covering of leaves of *Indigofera arrecta* Hochst. It is decidedly uncommon to find a *Pythium* species that may be considered a true epiphyte. A culture of this fungus was obtained from Baarn for study. The organism cor-

responds in all details with the description of the species and may be considered a type. Butler states that *P. indigoferae* ". . . is related to *P. gracile* in the structure of the sexual organs, but differs in the origin of the antheridium from the oogonial stalk." It differs further in possessing sporangia which are lobulate, usually occurring in the simple to complex aggregations of toruloid, dactyloid elements. The sexual apparatus is a distinctive feature of the species. In contrast to the majority of *Pythium* spp. in which the oogonial stalk is straight and the antheridium is curved toward it, the oogonial stalk of *P. indigoferae* is conspicuously curved toward the antheridium which consists of a straight branch. Additional distinction lies in the shape of the antheridial cell which is filamentous and only rarely somewhat inflated at its apex. There is only a delicate union between the apex of the antheridium and oogonial wall, the remaining portion of the antheridium being free. The antheridia of *P. indigoferae* are very similar to those of *P. torulosum* and further similarity with *P. torulosum* is evidenced in the asexual stage. *P. indigoferae* differs from *P. torulosum* in its oogonial disposition and aplerotic oospores.

As stated by Butler, the size of the oogonia in *Pythium indigoferae* is remarkably constant. Butler lists the oogonia as being 18 to 20 μ in diameter. Measurement of 200 oogonia made by the writer gave a range of 16.3 to 22.4 μ in diameter and a mean diameter of 19.2 μ. Oospore measurements agree with those reported by Butler.

Pythium deliense is the only other species of *Pythium* in which the oogonium is directed toward the antheridium. *P. deliense* may be distinguished morphologically from *P. indigoferae* by the absence of sexual organs in conjunction with sporangial complexes. The difference in the orientation of the sporangial emission tube of *P. deliense* and *P. indigoferae* as pointed out by Meurs (1934) is not a satisfactory criterion for specific identification. The emission tube of *P. indigoferae* is usually laterally directed, though occasional instances of terminal disposition have been observed. The writer concurs with the opinion of Meurs that the emission tube in *P. deliense* is usually terminal and rarely lateral; however, the use of variable morphologic features as criteria for the separation of closely related species should be avoided.

Both *Pythium indigoferae* and *P. deliense* exhibit a rosette habit of growth on solid nutrient media; the rate of growth at room temperature is also similar. A comparison of the respective optima and maxima temperatures for growth, however, reveals that they are very dissimilar; the maximum temperature for mycelial growth of *P. indigoferae* is 37° C. while that of *P. deliense* is 43° C. The temperature-growth relation of the two fungi constitutes a valuable factor in specific segregation.

Pythium indigoferae is listed from leaves of *Indigofera arrecta* Hochst. in India by Butler (1907), Butler and Bisby (1931) and Sydow and Butler (1907), from *Ananas comosus* Merr. by Sideris (1931) and according to Sideris obtained from roots of *Cucumis sativus* L. by McRae in India.

20. PYTHIUM DELIENSE Meurs, Phytopath. Zeit. 7: 169–185. 1934.

Hyphae abundantly and irregularly branched, measuring from 2.6 to 8.6 μ in diameter. Sporangia terminal, rarely intercalary, inflated filamentous, up to 210 μ long and of variable diameter but always larger than parent hypha, usually provided with inflated lateral branches, usually not forming intricate complexes; zoospores 3 to 25 or more, reniform, laterally biciliate, measuring 8 to 12 μ in diameter when encysted; the evacuation tube of variable length, usually of terminal origin though occasionally lateral. Oogonia spherical, terminal, smooth- and thin-walled, measuring 15 to 23.1 μ, mostly 16.1 to 20.0 μ, av. 18.2 μ, in diameter. Antheridia typically monoclinous, occasionally diclinous, usually single, rarely two per oogonium, the antheridial stalk usually straight, the oogonial branch and oogonium bent toward the antheridial cell, infrequently the two stalks are parallel branches of the same hypha, the antheridial cell is filamentous-clavate, terminal or intercalary, 12.8 to 27.0 μ, mostly 14.1 to 20.3 μ, long and 4.7 to 15.5 μ, mostly 8.1 to 11.4 μ, wide making apical contact with the oogonial wall. Oospores aplerotic, provided with a wall 0.9 to 2.2 μ, mostly 1.3 to 1.8 μ, average 1.62 μ thick, containing a single reserve globule and refringent body, oospore measuring 12.5 to 17.5 μ, mostly 13.7 to 16.2 μ, average 14.8 μ, in diameter.

Originally described as one of the causal agents of stemburn of *Nicotiana tabacum* L., Sumatra, N. E. I.

A study of the type culture was undertaken. As the work progressed, it became increasingly apparent that *Pythium deliense* and *P. indigoferae* are closely related species. The oogonia and oospores of *P. deliense* vary in size more than is indicated in Meurs' diagnosis: oogonia range from 12.1 to 31.3 μ, mean 18.9 μ, in diameter; oospores range from 10.2 to 23.2 μ, mean 15.3 μ, in diameter. The antheridia are appropriately described in the diagnosis.

No sexual organs were formed in connection with the sporangial complexes, substantiating the observation of Meurs.

As indicated in the discussion of *Pythium indigoferae*, *P. deliense* exhibits a sexual stage which is common to both species, namely the bending of the oogonial stalk and appended oogonium toward the antheridium. The antheridial stalk remains more or less straight; this phenomenon is in sharp contrast to the behavior of the other *Pythium* spp. in which the converse is the rule.

The emission tube in *Pythium deliense* is reported to arise most frequently in a terminal position, rarely laterally. The emission tube in *P. indigoferae* is, according to Meurs, laterally oriented. The writer has occasionally observed the emission tube to be acrogenous in *P. indigoferae*. As stated for *P. indigoferae*, it seems best to avoid the use of variable characteristics in the separation of closely allied species; contrary to Meurs' opinion, it is not necessary to rely upon this characteristic for specific identification.

Pythium deliense is also closely allied to *Pythium aphanidermatum*. The oogonia and oospores are very similar in size and shape and in instances where the oogonial stalk and oogonium are not directed toward the straight

antheridial stalk in *P. deliense*, as instances of parallel branches or diclinous antheridia, some difficulty in separation might be incurred were it not for differences in the character of the antheridial cells of the two species. Intercalary antheridia are common to both species but usually more frequent in *P. aphanidermatum* than in *P. deliense*. In *P. aphanidermatum*, these are usually formed in a parent filament rather than on a monoclinous lateral branch derived from the oogonial stalk; in any event the antheridial cell in *P. aphanidermatum* is typically broad and stout, barrel-shaped or suborbicular and usually sessile. Antheridial cells of *P. deliense* are much less broad and stout, are more slender and clavate, are not produced in the same manner as those of *P. aphanidermatum* and are typically stalked. These two species are further distinguished by their asexual reproductive structures, simple and sparingly branched and elongate in *P. deliense*, complex, much branched and forming lobulate aggregations in *P. aphanidermatum*.

Utilization of the temperature relations and the absence of any sexual apparatus in association with the asexual structures will suffice as a basis for segregating *Pythium deliense* from *P. indigoferae*. The oogonial and antheridial habit of *P. deliense* makes it impossible to confuse the species with other aplerotic forms such as *P. aphanidermatum*, *P. tardicrescens*, *P. volutum*, *P. aristosporum*, and *P. myriotylum*.

Pythium deliense, together with *P. aphanidermatum* and *P. myriotylum*, is one of the causal agents of tobacco stemburn, occurring in Sumatra. Heretofore the tobacco pathogens had been referred to as *Pythium* spp. or *Pythium debaryanum* by Jochems (1926, 1927a, b). In addition to the original description by Meurs, *P. deliense* has been reported from tobacco in Sumatra by Jochems (1934) and van der Weij (1935). Meurs believes that the fungus discussed by van Breda de Haan (1896) as *Phytophthora nicotianae* and subsequently believed to be derived from a mixed culture, contained as a component part the present described *Pythium deliense*.

21. PYTHIUM APHANIDERMATUM (Edson) Fitzpatrick, Jour. Agr. Res. **4**: 279–292. 1915.

Nematosporangium aphanidermatum (Edson) Fitzp. Mycologia **15**: 166–173. 1923.
N. aphanidermatum (Edson) Sideris, Mycologia **23**: 252–295. 1931.
N. aphanidermatum var. *hawaiiensis* Sideris, l.c.
Pythium butleri Subramaniam, Mem. Dept. Agr. India Bot. **10**: 181–194. 1919.
Rheosporangium aphanidermatus Edson, Jour. Agr. Res. **4**: 279–292. 1915; Mycologia **15**: 166–173. 1923.

Hyphae measuring 2.8 to 7.3 μ, largely 4 to 6 μ, in diameter, hyaline and nonseptate except in fructification. Sporangia (presporangia according to Edson) inflated filamentous, branched or unbranched, of varying length from less than 50 μ to more than 1000 μ and 4 to 20 μ wide, usually forming complexes; zoospores reniform, laterally biciliate, measuring about 12 μ long and 7.5 μ wide. Oogonia spherical, terminal, rarely intercalary, measuring 22 to 27 μ in diameter. Antheridia usually monoclinous but also diclinous, typically intercalary though often terminal, 1 to 2 per oogonium, barrel- or

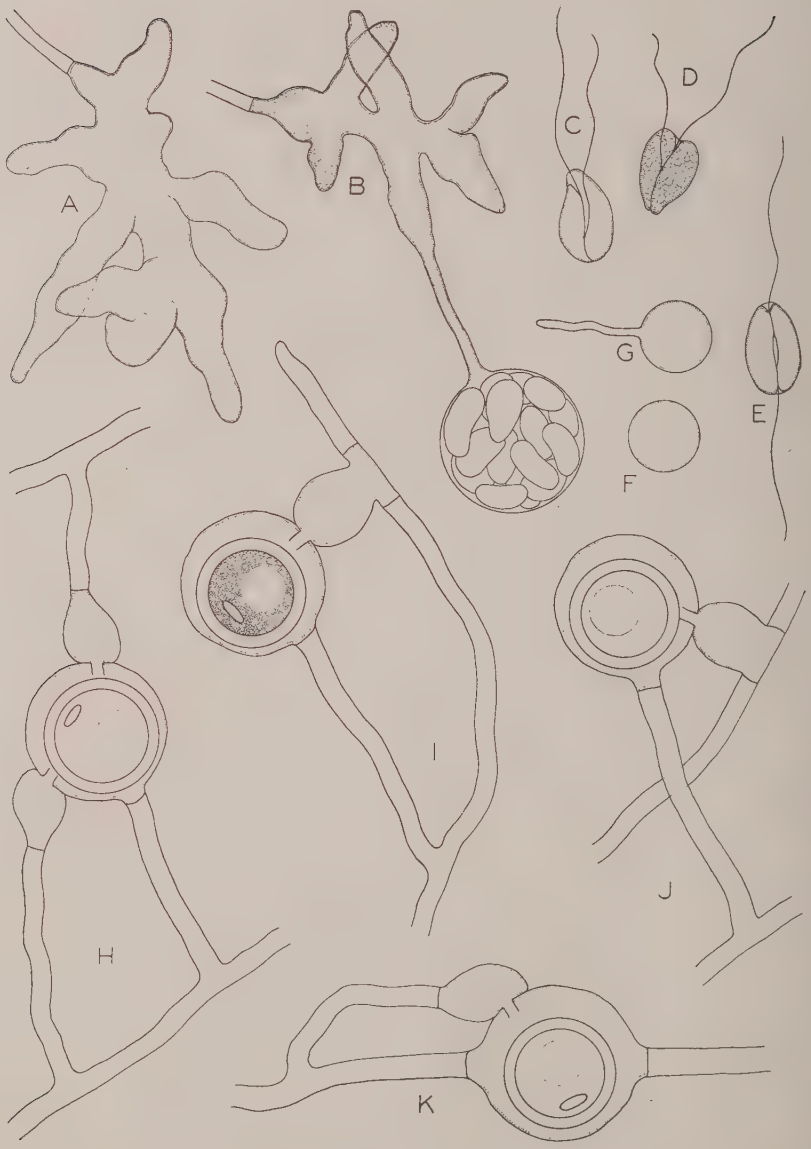

FIG. 3. *Pythium aphanidermatum*. *A–G*, Asexual stages. *A*, Inflated filamentous sporangium. *B*, Sporangium with vesicle containing zoospores. *C–E*, Zoospores. *F*, Encysted zoospore. *G*, Encysted zoospore producing germ tube. *H–K*, Sexual stages. *H*, *K*, Oogonia with terminal antheridia. *I*, *J*, Oogonia with intercalary antheridia.

dome-shaped, suborbicular, becoming cylindric or broadly clavate, usually measuring 9 to 11 μ by 10 to 14 μ, producing a conspicuous penetration tube. Oospores aplerotic, single, with a moderately thick wall, measuring 17 to 19 μ in diameter; germination by the production of a germ tube.

Originally described as pathogenic on *Beta vulgaris* L., U. S. A.

The diagnosis given above is taken in large part from Edson's paper in which he describes *Rheosporangium aphanidermatus* as a new genus and species of the Saprolegniaceae.

Carpenter (1921) working with pure cultures of the sugarcane *Pythium*, noted that his fungus agreed very closely in both the asexual and the sexual stages with the sugar beet root rot fungus *Rheosporangium aphanidermatus*. Carpenter states that ". . . it seems more natural to include this fungus (*R. aphanidermatus*) under the genus Pythium of the Pythiaceae. . . ." He also noted a rather close agreement of his fungus with *P. butleri*, considered a new species by Subramaniam (1919). In summarizing his work Carpenter says that he ". . . considers the cane fungus morphologically the same as *R. aphanidermatus* and *P. butleri*."

Coker (1923) in his monograph of the Saprolegniaceae concludes that there is no apparent reason for retention of the genus *Rheosporangium* in the Saprolegniaceae and that it is best placed in the genus *Pythium* in the Pythiaceae.

It was not until Fitzpatrick (1923) published his comments on generic concepts in the Pythiaceae that *Rheosporangium aphanidermatus* was transferred to the genus *Pythium* as *P. aphanidermatum* (Eds.) Fitzp.

Sporangia of *Pythium aphanidermatum* are typically lobulate, branched, inflated and rather freely produced in most culture media. Zoospore production occurs as described in the description above. Oogonia are usually terminal though occasionally intercalary, spherical, smooth, thin-walled. The antheridium is typically intercalary, barrel-shaped, dome-shaped or suborbicular, usually sessile on a supporting hypha. Acrogenous antheridia may also be present but are not as typical of the species as the intercalary antheridia. Oospores are aplerotic, smooth and moderately thick-walled, 1.0 to 2.0 μ in thickness.

A comparison of some measurements of the diameters of oogonia and oospores is tabulated below:

Author	*Host*	*Oogonia* (μ)	*Oospores* (μ)
Edson (1915)	Sugar beet	22–27	17–19
Meurs (1934)	Tobacco	16.7–28.7 av. 22.9	15.6–26.2 av. 20.5
Tasugi and Takatuzi (1935)	Bean	16.2–30.5 av. 23.3	12.4–24.8 av. 18.8
Writer	Bean	15.1–32.3 m. 26.0	12.1–28.4 m. 19.8
Writer	Sugar beet	16.3–29.9 m. 24.0	13.1–25.6 m. 19.0
Writer	Cucumber	16.8–34.2 m. 26.8	13.8–28.4 m. 21.3

Subramaniam (1919) described *Pythium butleri* as a new species of *Pythium* parasitic on ginger, tobacco, and papaya in India. This species was designed to replace type *c.* of *P. gracile*, described by Butler (1907) as a parasite of ginger and castor bean in India. In 1927 Mitra (1927) indicated that *P. butleri* and *P. aphanidermatum* are closely related but cannot be considered identical. A year later Mitra and Subramaniam (1928), as a result of a series of cross inoculations of fruits of various Cucurbitaceae with *P. butleri* and *P. aphanidermatum* consider the former merely a strain of the latter. Fitzpatrick, Ramakrishna-Ayyar (1929) and Butler and Bisby (1931) consider these two names synonymous. A comparative study of isolates of *P. aphanidermatum* and *P. butleri* conducted by the writer substantiates the conclusions of Fitzpatrick and the others mentioned above.

Drechsler (1934a) maintains that *Pythium butleri* and *P. aphanidermatum* should be kept as separate species; the writer is not in agreement with this. Drechsler's basis for separation is presented below: Sporangia of *P. aphanidermatum* are smaller, less extensive and less branched than those of *P. butleri;* the zoospores are likewise smaller in *P. aphanidermatum*, 9 μ opposed to 11 μ in diameter for *P. butleri*. The average diameter of oogonia and oospores of *P. aphanidermatum* is 22 μ and 17.5 μ respectively, compared with 27 μ and 22.5 μ respectively for *P. butleri*.

The values cited by Drechsler for *Pythium butleri* are not greatly different from those for *P. aphanidermatum* and cannot be considered significantly divergent. The morphology of cultures received by the writer as *P. butleri* is identical with that of the morphology of *P. aphanidermatum* cultures. Similarly, the growth-temperature relations of the two are identical.

Since *Pythium aphanidermatum* was described prior to *P. butleri*, the former is maintained as the valid binomial. This is in agreement with the work of Fitzpatrick and Matthews.

In addition to the morphologic peculiarities of *Pythium aphanidermatum* which distinguish this fungus from related species, the general growth habit and temperature relations may be utilized in some instances as an aid to specific identification. In contrast to the rosette growth habit of *P. indigoferae* and *P. deliense*, the mycelial development of *P. aphanidermatum* is haphazardly disposed, forming a copious amount of loosely arranged aerial hyphae. *P. tardicrescens*, *P. volutum*, and *P. aristosporum* have an appressed aerial mycelium which develops slowly in comparison with the rapidly produced, abundant aerial mycelium of *P. aphanidermatum*. *P. myriotylum* and *P. aphanidermatum* are indistinguishable macroscopically. The growth-temperature values for *P. aphanidermatum*, *P. deliense*, and *P. myriotylum* are very similar and distinctly different from those of *P. tardicrescens*, *P. volutum*, and *P. aristosporum*.

The host range of *Pythium aphanidermatum* includes the following listed plants:

Agave rigida var. *sisalana* Perr. KENYA: McDonald (1932).
Agrostis stolonifera L. UNITED STATES: Monteith (1933).
Amaranthus sp. MALAYA: Milsum and Grist (1941); Sharples (1929).
A. gangeticus L. INDIA: Butler and Bisby (1931).
Amorphophallus sp. INDIA: Butler and Bisby (1931); Sundaraman (1926–27).
Ananas comosus Merr. HAWAII: Martin (1933); Parris (1940); Sideris (1931).
Armoracia rusticana Gaertn. UNITED STATES: Nance (1940).
Basella sp. INDIA: Butler and Bisby (1931); Sundaraman (1926–27).
Benincasa hispida Cogn. CHINA: Yu (1934, 1940).
Beta vulgaris var. *macrorhiza* Stev. AUSTRALIA: Simmonds (1933). AUSTRIA: Fischer (1931); Miestinger *et al.* (1932). CHINA: Yu (1934, 1940). UNITED STATES: Edson (1915a, 1915b); Durrell (1939); Kreutzer and Durrell (1938); Middleton (1938); Nance (1939).
B. vulgaris var. *cicla* L. UNITED STATES: Matthews (1931).
Brassica chinensis L. CHINA: Yu (1934).
B. oleracea var. *capitata* L. CHINA: Yu (1934). INDIA: Ramakrishna-Ayyar (1929). UNITED STATES: Drechsler (1925b).
Cannabis sativa L. INDIA: Galloway (1937).
Capsicum annuum L. CHINA: Yu (1934). INDIA: Butler and Bisby (1931); McRae (1928); Mitra (1925); Mitra and Subramaniam (1928); Subramaniam (1919). UNITED STATES: Author.
Carica papaya L. HAWAII: Jones *et al.* (1941); Parris (1940); Sideris (1931, 1935). INDIA: Bhargava (1941); Butler and Bisby (1931); Mitra (1925); Mitra and Subramaniam (1928); Subramaniam (1919). PUERTO RICO: Seaver *et al.* (1932). UNION SOUTH AFRICA: Doidge and Bottomley (1931); Wager (1931, 1932a, 1933, 1940). UNITED STATES: Author.
Citrullus vulgaris Schrad. BALUCHISTAN: Kheswalla (1936). CHINA: Teng (1935); Yu (1934, 1940). UNITED STATES: Drechsler (1925c); Gottlieb and Butler (1939); Author.
Colocasia antiquorum Schott. GOLD COAST: Wright (1931).
Cucumis melo L. CHINA: Yu (1934). UNITED STATES: Drechsler (1925c); Gottlieb and Butler (1939); Author.
C. melo var. *inodoratus* Naud. UNITED STATES: Drechsler (1925c); Author.
C. melo var. *momordica* Roxb. INDIA: Mitra (1927); Mitra and Subramaniam (1928).
C. melo var. *reticulatus* Naud. UNITED STATES: Gottlieb and Butler (1939); Author.
C. sativus L. CHINA: Yu (1934, 1940). INDIA: Butler and Bisby (1931); McRae (1923, 1924); Mitra (1927); Mitra and Subramaniam (1928). ITALY: Petri (1931). JAPAN: Darker (1940); Tasugi and Takatuzi (1935). PALESTINE: Reichert (1939). POLAND: Garbowske and Juraszkówna (1933); Siemaszko (1931). PUERTO RICO: Alvarez (1941). UNITED STATES: Drechsler (1925c); Gottlieb and Butler (1939); Nance (1939); Ramsey (1939); Author.
Cucurbita sp. POLAND: Siemaszko (1931).
C. moschata Duchesne. CHINA: Yu (1934).
C. pepo L. UNION SOUTH AFRICA: Wager (1932a, 1940). UNITED STATES: Drechsler (1925c); Author.
C. pepo var. *condensa* Bailey. UNITED STATES: Drechsler (1925c); Gottlieb and Butler (1939); Author.
Curcuma longa L. CEYLON: Park (1934).
Datura sp. INDIA: Butler and Bisby (1931); Sundaraman (1926–27).
D. fastuosa L. JAPAN: Tasugi and Takatuzi (1935).
Daucus carota L. UNITED STATES: Gottlieb and Butler (1939).
Euphorbia antiquorum L. INDIA: Ramakrishna-Ayyar (1929).
Festuca sp. CYPRUS: Nattrass (1936).
Ficus carica L. JAPAN: Tasugi and Takatuzi (1935).
Gaillardia sp. MALAYA: Thompson (1939).
Gossypium sp. ANGLO-EGYPTIAN SUDAN: Andrews and Clouston (1938); Massey (1936).
G. hirsutum L. CHINA: Teng (1935).
Ipomoea batatas Lam. UNION SOUTH AFRICA: Wager (1931). UNITED STATES: Gottlieb and Butler (1939); Harter and Whitney (1927b); Lauritzen, Harter and Whitney (1933); Nance (1940); Author.

Lactuca sativa var. *angustana* Irish. CHINA: Teng (1937).
Lagenaria leucantha Rusby. CHINA: Yu (1934). INDIA: Butler and Bisby (1931); McRae (1923); Mitra (1927); Mitra and Subramaniam (1928).
Lepidium sativum L. MALAYA: Milsum and Grist (1941).
Linum usitatissimum L. NETHERLANDS: Diddens (1932).
Luffa acutangula Roxb. INDIA: Butler and Bisby (1931); McRae (1923); Mitra (1927); Mitra and Subramaniam (1928).
L. aegyptiaca Mill. INDIA: Butler and Bisby (1931); McRae (1923); Mitra (1927); Mitra and Subramaniam (1928).
L. cylindrica Roem. CHINA Yu (1934, 1940).
Lycopersicon esculentum Mill. CHINA: Yu (1934). INDIA: Ramakrishna-Ayyar (1929). MALAYA: Tempany (1934). PALESTINE: Reichert (1939). UNION SOUTH AFRICA: Wager (1931, 1932a, 1933, 1940). UNITED STATES: Brown (1940); Gottlieb and Butler (1939); Author.
Momordica balsamina L. CHINA: Yu (1934).
M. charantia L. INDIA: Mitra (1927); Mitra and Subramaniam (1928).
Nicotiana tabacum L. CHINA: Yu (1934). GOLD COAST: Bunting and Dade (1924); Symond (1939). INDIA: Butler and Bisby (1931); Galloway (1935); Mitra (1925); Mitra and Subramaniam (1928); Subramaniam (1919); Venkatarayan (1937). NYASALAND: Hornby (1933). RHODESIA: Hopkins (1939a). SUMATRA: Drechsler (1926); Jochems (1926, 1927); Meurs (1934); van der Goot (1935, 1937); van der Weij (1935); van Hall (1925). TOGOLAND: Bunting (1924). UNION SOUTH AFRICA: Wager (1931, 1932a, 1933, 1940). UNITED STATES: Anderson *et al.* (1939).
Opuntia dillenii Haw. INDIA: Butler and Bisby (1931); Ramakrishna-Ayyar (1929); Sundaraman (1926–27).
Phaseolus aureus Roxb. UNITED STATES: Author.
P. limensis Macf. UNITED STATES: Author.
P. vulgaris L. JAPAN: Asuyama (1935); Tasugi and Takatuzi (1935). UNITED STATES: Harter and Zaumeyer (1931a, 1931b); Lauritzen, Harter and Whitney (1933); McLaughlin (1942); Zaumeyer (1930).
Physalis sp. INDIA: Butler and Bisby (1931); Sundaraman (1926–27).
Picea engelmanni Engelm. UNITED STATES: Rathbun (1923); Rathbun-Gravatt (1925, 1931); Gravatt (1925).
Pinus banksiana Lamb. UNITED STATES: Hartley (1921); Hartley, Merrill and Rhoads (1918); Rathbun (1922, 1923); Rathbun-Gravatt (1925, 1931).
P. resinosa Ait. UNITED STATES: Gravatt (1925); Rathbun (1922, 1923); Rathbun-Gravatt (1925, 1931).
Poa sp. UNITED STATES: Monteith (1933).
Pseudotsuga taxifolia Britt. UNITED STATES: Eliason (1928).
Pteridium aquilinum Kuhn. UNION SOUTH AFRICA: Wager (1933, 1940).
Pyrus malus L. UNITED STATES: Gottlieb and Butler (1939).
Raphanus sativus L. CHINA: Yu (1934). UNITED STATES: Brown (1940); Edson (1915b); Edson and Wood (1936, 1937); Gardner (1925); Nance (1939); Vaughn (1924).
R. sativus var. *longipinnatus* Bailey. UNITED STATES: Gardner (1925); Gregory (1925).
Ricinus communis L. INDIA: Butler (1907); Butler and Bisby (1931); Subramaniam (1919).
Saccharum officinarum L. HAWAII: Agee (1932); Bourne (1924); Carpenter (1921, 1928a, c, 1930); Heck (1934); Martin (1930, 1931, 1934); Sideris (1935). PHILIPPINE ISLANDS: Agati (1931). PUERTO RICO: Bourne (1924); Cook (1939). UNITED STATES: Drechsler (1934a); Rands (1930); Rands and Dopp (1938b); Stevenson and Rands (1938); Tims (1932b).
Secale cereale L. CHINA: Teng (1935).
Sechium edule Sw. UNION SOUTH AFRICA: Wager (1932a, 1933, 1940).
Solanum sp. INDIA: Butler and Bisby (1931); Sundaraman (1926–27).
S. melongena L. CHINA: Yu (1940). INDIA: Ramakrishna-Ayyar (1929). UNION SOUTH AFRICA: Wager (1933, 1940). UNITED STATES: Drechsler (1926); Gottlieb and Butler (1939); Author.
S. tuberosum L. CYPRUS: Nattrass (1936, 1937). INDIA: Butler and Bisby (1931); Ramakrishna-Ayyar (1929); Subramaniam (1919). UNION SOUTH AFRICA: Doidge and Bot-

tomley (1931); Wager (1931, 1932a, 1932b, 1933, 1940). UNITED STATES: Nance (1940); Author.
Sorghum vulgare Pers. var. *sudanense* (Piper) Hitchc. HAWAII: Martin (1934).
Spinacea oleracea L. UNITED STATES: Drechsler (1938).
Tephrosia toxicaria Pers. MALAYA: Sharples (1930).
Trichosanthes anguina L. INDIA: Butler and Bisby (1931); McRae (1923, 1924); Mitra (1927); Mitra and Subramaniam (1928).
T. dioica Roxb. INDIA: Butler and Bisby (1931); McRae (1924); Mitra (1927); Mitra and Subramaniam (1928).
Viola tricolor L. NETHERLANDS: van Eek (1938).
Vitis vinifera L. UNITED STATES: Gottlieb and Butler (1939).
Xanthosoma sagittifolium Schott. GOLD COAST: Wright (1931).
Zea mays L. PHILIPPINE ISLANDS: Agati (1931). UNITED STATES: Altstatt (1942); Nance (1939, 1940); Author.
Zingiber officinale Roscoe. CEYLON: Park (1934). INDIA: Butler (1907); Butler and Bisby (1931); Mitra and Subramaniam (1928); Sen (1930); Subramaniam (1919); Thomas (1938).
Zinnia sp. MALAYA: Sharples (1929); Thompson (1931).

The occurrence of *Pythium aphanidermatum* on radish is questioned by Kendrick (1927), who states the disease to be due to *Aphanomyces raphani* Kendrick.

22. PYTHIUM TARDICRESCENS Vanterpool, Ann. Appl. Biol. **25**: 528–543. 1938.

Hyphae measuring mostly 2.5 to 5 μ in diameter, irregularly branched, frequently forming knob-like appressoria. Sporangia inflated filamentous, toruloid or moderately lobed, never producing complex lobulations; zoospores not observed, the sporangium germinating by means of germ tubes which may terminate in a spherical body (conidium, according to Vanterpool). Oogonia spherical, terminal on short branches, rarely intercalary, measuring 17 to 30 μ, average 24.1 μ, in diameter, containing several oil globules. Antheridia commonly monoclinous though also diclinous, 1 to 6, usually 2 to 3, per oogonium, clavate or crook-necked, 6 to 8.5 μ wide and 16 μ long, making narrow or moderate oogonial contact. Oospores aplerotic, single, with a moderately thick wall, 1.25 to 2 μ thick, containing a central reserve globule embedded in a finely granular matrix, oospores measuring 16 to 26 μ, average 20.3 μ, in diameter; germination not observed.

Originally isolated from diseased roots of *Triticum aestivum* L., Canada.

Pythium tardicrescens is described by Vanterpool as a new member of the lobulate sporangial congeners causing browning root rot of graminicolous hosts; the diagnosis given above is taken from the original work.

The description of the fungus is sufficiently complete and further discussion of the morphological features is unnecessary. The observations of the writer on isolates of this species obtained from Vanterpool concur with the remarks made by him. The fungus has an appressed, radiate, non-lustrous growth on nutrient agars. The rate of growth is slower than in any other lobulate diverticulate form in the writer's collection; the maximum temperature value is likewise the lowest of the group.

Pythium tardicrescens may be separated from congenerics which possess monoclinous, occasionally diclinous, antheridia in that the oogonial branch

is not curved toward the antheridium as in *P. indigoferae* and *P. deliense*. *P. tardicrescens* may be distinguished from *P. aphanidermatum* by its antheridial cells which are typically terminal, not greatly inflated, varying in number from one to six, usually two to three, per oogonium. These are in contrast to the typically intercalary, though occasionally acrogenous, antheridial cells which are inflated and vary from one to two, usually one, per oogonium in *P. aphanidermatum*. *P. indigoferae*, *P. deliense*, *P. aphanidermatum*, and *P. tardicrescens* all possess aplerotic oospores.

The temperature-growth relations of this species may be used as an additional basis for specific segregation.

This species is known to cause a root rot of wheat, *Triticum aestivum* L., in Canada and England and is stated to be ". . . pathogenic to other cereals and certain grasses when artificially inoculated . . ." according to Vanterpool (1938); this fungus is further associated with the browning root rot of wheat by Vanterpool in subsequent papers (1940a, 1940b).

23. Pythium volutum Vanterpool and Truscott, Canad. Jour. Res. 6: 68–93. 1932.

Hyphae measuring 2.0 to 5.5 μ in diameter. Sporangia inflated filamentous consisting of small lobulations or toruloid outgrowths; zoospores produced in meagre to moderate numbers, about 10 to 14 μ in diameter. Oogonia spherical to subspherical, smooth- and thin-walled, terminal on short lateral branches, rarely intercalary, measuring 19.5 to 40.2 μ, average 30 μ, in diameter. Antheridia typically diclinous, rarely monoclinous, producing 3 to 10 antheridia per oogonium, a single stalk producing as many as four antheridial cells which are straight or crook-necked, clavate, making narrow apical contact with the oogonium. Oospores aplerotic, single with a smooth, thickened wall about 2 μ thick, containing 1, and occasionally 2, reserve globule, and a single refringent body, the oospore measuring 14.7 to 36.4 μ average 27.7 μ, in diameter; germination not observed.

Originally isolated from roots of *Triticum aestivum* L., and *Avena sativa* L., Canada.

Cultures of *Pythium volutum* were secured from Vanterpool; this species is unique among the present known congeners with inflated diverticula. The species may be distinguished from others on the antheridial character alone. The antheridial branch is usually diclinous in origin and is helicoidally disposed about the oogonial stalk. The antheridial cells per antheridial stalk vary from one to four in number. When plural antheridia are present, rarely more than two of the antheridial stalks are entwined about the stalk of the oogone; usually only a single antheridial branch coils about the supporting oogonial branch.

Pythium volutum is easily cultivated on nutrient agar substrates with the production of moderately abundant aerial development and a more or less radially disposed mycelium. Like *P. tardicrescens*, *P. volutum* is a moderately slow growing species. The macroscopic aspect of mycelial development of

P. volutum resembles that of many strains of *P. arrhenomanes*, though *P. volutum* is quite distinct morphologically from *P. arrhenomanes*. The difference between the two species is further borne out by their temperature-growth responses as reported recently by Vanterpool (1938) and confirmed by the writer.

Pythium volutum, in addition to attacking *Triticum aestivum* L. and *Avena sativa* L. in Canada, attacks *T. aestivum* in England (Vanterpool, 1938); *P. volutum* can infect *Hordeum vulgare* L., *Secale cereale* L. and *Zea mays* L., when artificially inoculated (Bisby *et al.* 1938) and (Vanterpool and Truscott, 1932). van Luijk (1934a, 1938a) isolated this species from *Agrostis stolonifera* L., *Festuca duriuscula* L., and *Lolium annuum* var. *westerwoldicum* in the Netherlands.

24. PYTHIUM ARISTOSPORUM Vanterpool, Ann. Appl. Biol. **25**: 528–543. 1938.

Hyphae measuring 2.5 to 6.5 μ in diameter, producing numerous appressoria. Sporangia inflated filamentous, digitate, lobulate, simple or complex, usually germinating by production of germ tubes, though rarely producing reniform, biciliate zoospores, about 10 to 12 μ in diameter when encysted. Oogonia subspherical, smooth- and thin-walled, usually acrogenous on short lateral branches, intercalary, measuring 21 to 36 μ, average 28.8 μ, in diameter. Antheridia diclinous and monoclinous, usually 3 to 6, though as many as 8 or more, clavate, crook-necked, 6.8 μ wide and 17.4 μ long, making narrow to moderate apical contact with the oogonial wall; a single antheridial branch may supply as many as 4 antheridial cells, the whole forming entanglements about the oogonium, though vegetative prolongations are rare. Oospores aplerotic, single with a smooth, dark wall 1.5 to 2.0 μ thick, containing a single reserve globule and refringent body, oospore measuring 13 to 30 μ, average 24.2 μ, in diameter.

Originally isolated from roots of *Triticum aestivum* L., Canada.

Pythium aristosporum was reported by Vanterpool as a companion fungus to *P. tardicrescens* in causing the browning root rot of graminicolous hosts. The diagnosis presented above is taken from Vanterpool. As in *P. tardicrescens*, the writer's observations are limited to a study of isolates received from Vanterpool, and the observations of the writer agree with his description.

Pythium aristosporum differs from *P. tardicrescens* not only in its macroscopic appearance and temperature-growth response, but in certain morphologic details. Slight aerial development on nutrient agar substrates is common to both species. In *P. aristosporum*, however, there is no definite radial disposition of hyphae, the whole developing a granular, creamy-yellow appearance after several days' growth. The writer concurs with Vanterpool's observation that the rate of growth of *P. aristosporum* exceeds that of *P. tardicrescens;* further, that the maximum temperature for growth is higher. As stated by Vanterpool, *P. aristosporum* shows affinity to *P. myriotylum* in its antheridial disposition; in addition, *P. aristosporum* is also closely allied to *P. volutum* in possessing diclinous, and occasional mono-

clinous, antheridia. *P. aristosporum* differs from *P. volutum* in the non-helicoid antheridial branch. *P. myriotylum* and *P. aristosporum* may be distinguished morphologically on the basis of their antheridia. In *P. myriotylum* the antheridial branch does not originate in close proximity to the oogonium; the antheridial cells are crook-necked, not fully laterally adnate, rather making only basal and apical contact with the oogonium; vegetative prolongations of the anteridial branch are quite common. *P. aristosporum*, on the contrary, has an antheridial branch which arises in close proximity to the oogonium, possesses antheridial cells which are also crook-necked but which make only apical contact with the oogonium; vegetative prolongations of the antheridial branch are quite rare.

Further differences between *P. aristosporum* and *P. myriotylum* are found in their temperature-growth responses and growth habits.

Pythium aristosporum is known to parasitize roots of *Triticum aestivum* L. in Canada, and to be pathogenic to *Avena sativa* L., *Hordeum vulgare* L., and *Secale cereale* L. upon inoculation. Fischer *et al.* (1942) report this species from *Agropyron trachycaulum* (Link) Malte and *Echinochloa crus-galli* (L.) Beauv., Vanterpool and Sprague (1942) report the fungus from *Hordeum vulgare* L. and *Triticum aestivum* L. and Sprague adds *Dactylis glomerata* L., all from the United States.

25. Pythium myriotylum Drechsler, Jour. Wash. Acad. **20**: 398–418. 1930.

Hyphae measuring 2.5 to 8.5 μ in diameter, when young mostly 3 to 4 μ, when old mostly 7 to 8.5 μ in diameter; forming numerous clavate or knob-like appressoria measuring 7 to 11 μ in diameter. Sporangia terminal or intercalary, sometimes undifferentiated though generally including an inflated filamentous lobulate or digitate lateral element, the undifferentiated portions measuring 0.1 to 0.3 mm. in length and 3 to 7 μ in diameter, the inflated portions of variable size, 10 to 175 μ in length and 12 μ in diameter; evacuation tube arising either from the undifferentiated or inflated portion, 10 to 100 μ long and 2 to 3.5 μ wide; 3 to 40 zoospores formed in the apical vesicle, reniform and laterally biciliate, 9 to 16 μ, average 11 μ, in diameter, germinating by a single germ tube. Oogonia spherical to subspherical, smooth- and thin-walled, terminal or intercalary, measuring 15 to 44 μ, average 26.5 μ, in diameter. Antheridia typically diclinous, when monoclinous usually originating in excess of 100 μ from the oogonium, 1 to 10, usually 3 to 6, per oogonium, the antheridial cell terminally expanded, clavate, crook-necked, arched, measuring 8 to 30 μ long and 4 to 8 μ wide, the apex making narrow apical contact with the oogonial wall, the middle arched upward and the proximal end frequently contacting the oogonial wall. Oospores aplerotic, single, with a wall 1 to 2 μ thick, containing a single reserve globule and a subspherical or strongly flattened refringent body, oospores measuring 12 to 37 μ, average 20.8 μ, in diameter.

Cause of fruit rot of *Citrullus vulgaris* Schrad., *Cucumis sativus* L. and *Solanum melongena* L., and decaying rootlets of *Lycopersicon esculentum* Mill. in U. S. A.

A study of the type culture, an isolate from *Nicotiana tabacum* L. in Sumatra and a culture from *Carica papaya* L. from South Africa was made.

The observations of the writer agree in all respects with the delimitations of the species as given by Drechsler. The Sumatran isolate, as stated by Meurs (1934), has oogonia which are slightly larger than those cited by Drechsler, 21.2 to 38.1 μ, mostly 26.1 to 32.1 μ, mean 28.6 μ in diameter. The South African isolate measured 19 to 38.5 μ, mostly 22.1 to 29.6 μ, mean 25.7 μ in diameter. The sporangia of the tobacco and papaya strains conformed with those of the type culture. The antheridia of all three isolates were comparable, varying from 1 to 10, usually 3 to 6, in number, of diclinous origin, occasionally monoclinous. The antheridial cell is uniquely applied to the oogonium, making basal and apical contact, the middle part arched outward and free from the oogonium. Vegetative prolongations on the antheridial branches are commonly observed.

The fungus grows rapidly at room temperature on suitable agar substrates. The high maximum temperature for growth dismisses any confusion with congeners with aplerotic oospores, such as *Pythium aristosporum*, *P. volutum*, *P. tardicrescens*, and *P. indigoferae*.

Pythium myriotylum, *P. deliense*, and *P. aphanidermatum* all have high maxima growth temperatures and cannot be segregated on this basis alone; morphological differences must be employed to separate the three species. The oogonium in *P. myriotylum* is not inclined toward the oogonium as in *P. deliense*. The typically intercalary antheridia of *P. aphanidermatum* are absent in *P. myriotylum*..

So far as the writer is aware, *Pythium myriotylum* has been encountered only in the warmer climates; these areas and the hosts from which the fungus is known are listed below: *Carica papaya* L. by Wager (1932a, 1940) in South Africa; *Citrullus vulgaris* Schrad., *Cucumis sativus* L., and *Lycopersicon esculentum* Mill. by Drechsler (1930a) in southeastern United States; *Nicotiana tabacum* L. by Jochems (1934), Meurs (1934) and van der Weij (1935) in Sumatra; *Phasoleus vulgaris* L. (inoculation) by Harter and Whitney (1927a) in the United States; probably this species by Deighton (1936) in Sierra Leone; seedling root rot of *Robinia pseudo-acacia* L. by Weiss (1942) in the United States; *Solanum melongena* L. by Drechsler (1930a) in the United States; *Zingiber officinale* Roscoe by Park (1937, 1941) in Ceylon, by Uppal (1940) in India.

26. PYTHIUM PERIPLOCUM Drechsler, Jour. Wash. Acad. **20**: 398–418. 1930.

Hyphae measuring 1.5 to 9 μ, mostly 1.8 to 4.2 μ, in diameter, irregularly and abundantly branched. Sporangia inflated filamentous, usually intercalary though often acrogenous, digitate, lobulate elements 10 to 30 μ long and 8 to 20 μ wide, simple, or 20 to 40 elements grouped to form intricate moriform aggregations; zoospores few to 125 in a vesicle, broadly reniform, laterally biciliate, measuring 8 to 11 μ in diameter upon encystment. Oogonia spherical to subspherical, provided with an echinulate wall, the spines 2 to 4 μ, average 2.8 μ, in length and 1.4 to 3 μ, average 1.8 μ, at the base, tapering slightly to a rounded apex, the oogonia acrogenous or intercalary, measuring

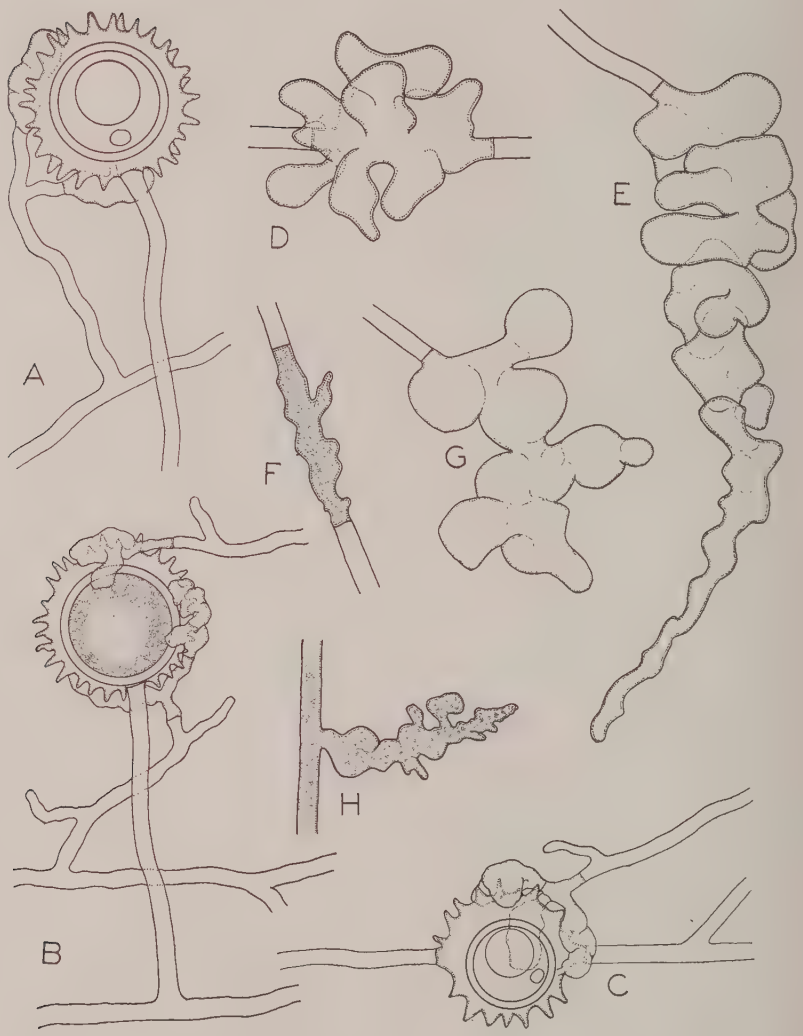

FIG. 4. *Pythium periplocum*. *A–C*, Sexual apparatus. *A*, *B*, Acrogenous oogonia with lobate diclinous antheridia. *C*, Intercalary oogonium with 3 antheridial cells from a single diclinous stalk. *D–H*, Sporangia. *D*, Intercalary sporangium. *E*, *G*, Terminal moriform type sporangia. *F*, immature intercalary sporangium. *H*, Immature acrogenous sporangium.

13 to 32 μ, average 24.6 μ, in diameter, not including the spiny protuberances. Antheridia diclinous, 1 to 4 in number, usually originating from 1 to 2 stalks, the antheridial cell sometimes clavate, more often long, 15 to 30 μ, and markedly lobed, the lobes 5 to 10 μ long and 5 to 8 μ wide, making ventral contact with the oogonial wall, antheridia and distal portion of the antheridial stalks intricately and extensively wrapped about the oogonium. Oospores aplerotic, single, spherical with smooth, thin wall measuring 0.7 to 1.9 μ, average 1.4 μ, in thickness and containing a single reserve globule and subspherical or flattened refringent body, the oospore measuring 11.5 to 27 μ, average 21.2 μ, in diameter.

Originally described from decayed fruits of *Citrullus vulgaris* Schrad. in the United States.

Pythium periplocum is at present the only known species of *Pythium* possessing filamentous sporangia that also possess echinulate oogonia.

In addition to the paper in which the species is described, Drechsler (1939) gives a more recent and elaborated account of the morphology and habit of the fungus.

The observations of the writer are in agreement with the detailed diagnosis of Drechsler. In culture on solid nutrient agar substrates, *Pythium periplocum* produces a moderate amount of aerial mycelium which has a peculiar cumulous aspect; small tufts of the aerial mycelium are aggregated to form a spherical, raised, hyphal mass. No other filamentous species of *Pythium* exhibits this habit in culture. The identical habit is expressed, however, in cultures of *P. acanthicum*, a member of the group of species possessing spherical sporangia, but is unknown in any other species of the group.

The hosts from which this species is known are: *Citrullus vulgaris* Schrad., Drechsler (1930a, 1939), *Cucumis melo* L. var. *reticulatus* Naud. and *C. melo* var. *inodoratus* Naud., author, *Prunus serotina* Erhr., Drechsler (1939) in the United States, and from *Gossypium* sp. in the Anglo-Egyptian Sudan by Andrews and Clouston (1938).

27. PYTHIUM SALPINGOPHORUM Drechsler, Jour. Wash. Acad. **20**: 398–418. 1930.

Hyphae measuring 1.5 to 7.0 μ, mostly 2 to 5.5 μ, in diameter; appressoria are clavate, 7 to 8.5 μ at their apex, frequently forming connected systems of falcate elements. Sporangia spherical to subspherical, usually formed in abundance, terminal, subterminal or intercalary, measuring 17 to 33 μ, average 24 μ, in diameter, usually proliferous, the secondary sporangium borne within the primary one; zoospores 15 to 40, longitudinally grooved and biciliate, broadly reniform, measuring 7.5 to 9.2 μ, average 8.5 μ, in diameter upon encystment. Oogonia spherical to subspherical, terminal, intercalary or tangentially intercalary, often forming a series of 2 to 5, smooth- and thin-walled, often including a portion of the supporting stalk, measuring 11 to 22 μ, average 15.8 μ, in diameter, excluding the attached plugs; approximately 75 percent of the oogonia develop parthenogenetically. Antheridia typically monoclinous, though also diclinous, 1 rarely 2, per

oogonium, when diclinous often lateral, sessile and straight, when monoclinous, proximal to the oogonium and strongly crook-necked, either type measuring 10 to 20 μ long and 3.5 to 6 μ wide, either delimited or undelimited by a septum; antheridia often lacking or non-functional. Oospores plerotic, the oospore wall usually fused with the oogonial wall, single, measuring 10 to 19 μ, average 14.6 μ, in diameter, with a thin wall, measuring 0.8 to 1.5 μ, average 1.2 μ, thick, containing a single reserve globule and refringent body.

Originally isolated from decaying roots of *Pisum sativum* L., United States.

The observations of the writer are confined to the study of two isolates which agree with the description of the fungus as given above.

Pythium salpingophorum presents many peculiarities which assist in its ready identification. It is the only species possessing plerotic oospores which has proliferous sporangia. The intercalary oogonia resemble those of *P. debaryanum*, having a short filamentous portion of the hypha attached to the oogonium, the whole being more or less prolate-limoniform. The oospores of *P. salpingophorum*, however, are quite different from those of *P. debaryanum*, being plerotic and usually fusing indistinguishably with the wall of the spherical part of the oogonium whereas those of *P. debaryanum* are aplerotic and not fused with the oogonial wall.

A large number of the oospores of *Pythium salpingophorum* are apandrous while others are parthenogenetic despite the presence of an antheridium; the antheridia present in the latter case are usually not delimited by a septum and lack a fertilization tube. The antheridia present closely resemble those of *P. ultimum;* the species may be distinguished from *P. ultimum* by its plerotic oospores and proliferous sporangia.

Further relationship of *Pythium salpingophorum* and *P. debaryanum* is evident in their temperature-growth relationships and growth habits.

In addition to the isolation of the fungus from roots of *Pisum sativum* L. by Drechsler, the author has obtained it from roots of *Ceanothus cyaneus* Eastw. and *Lycopersicon esculentum* Mill.

28. Pythium conidiophorum Jokl, Öst. Bot. Zeits. **67**: 33–37. 1918.

Hyphae non-septate, measuring 2 to 6.3 μ in diameter. Sporangia are spherical, terminal on long branches up to 100 μ in length, varying in size from 8 to 20 μ in diameter, germinating by germ tubes. Oogonia are spherical, terminal, usually borne on short lateral branches, 6.3 to 15.9 μ in diameter. Oospores are plerotic and apandrous.

Parasitic on *Spirogyra dubia* Kütz., *S. communis* (Haas.) Kütz., and *S. varians* Kütz., Albania.

The diagnosis given above was condensed from the original German text published by Jokl.

Pythium conidiophorum is readily distinguished from its congeners *P. hypogynum*, *P. rostratum*, and *P. iwayamai* in possessing apandrous oospores. The sporangia are reported to be frequently deciduous, always germinating

by means of germ tubes; these structures are termed conidia by Jokl and they are without doubt the most analagous reproductive bodies to conidia in the genus. Just what disposition should be made regarding these structures and further identity of the species is questionable due to the rather brief discussion of the organism and the fact that this species has not been observed subsequent to its description.

No hosts other than those from which the species was originally described have been reported.

29. PYTHIUM HYPOGYNUM Middleton, sp. nov.

Hyphae non-septate when young, irregularly septate when old, measuring 1.5 to 8.3 μ, average 5.1 μ, in diameter. Sporangia terminal, rarely intercalary, spherical to subspherical, smooth- and thin-walled, measuring 6.5 to 34.6 μ, average 22.1 μ, in diameter, sporangia germinating by means of germ tubes or zoospores. Oogonia terminal, spherical to subspherical, smooth- and thin-walled, measuring 10.2 to 35.1 μ, average 22.0 μ, in diameter. Antheridia hypogynous, single, delimited within the oogonial stalk at a distance varying from 5 to 30 μ below the oogonium; antheridial cell small, 2.8 to 8.3 μ, average 5.4 μ, wide, 3.0 to 11.1 μ, average 6.6 μ, long, supplied with a tenuous fertilization tube that just penetrates the oogonial wall. Oospores plerotic, smooth-walled, containing a single reserve globule and a prolate ellipsoidal or flattened refringent body; oospore germination not observed.

Isolated from decayed roots of *Hordeum vulgare* L., Missouri, U. S. A.

Hyphae juvenes non septatae, veteres irregulariter septatae, 1.5–8.3 μ diam.; sporangia terminalia, rare interposita, globosa vel subglobosa, cuticula levi tenuique, 6.5–34.6 μ diam., tubulis vel zoosporis germinantia. Oogonia terminalia, globosa vel subglobosa, membrana levi tenuique, 10.2–35.1 μ diam. Antheridia hypogyna, solitaria, sub oogonio 5–30 μ in stipite eiusdem delimitata; antheridii cellula parva, 2.8–8.3 μ lata, 3.0–11.1 μ longa, oogonii membranam appendicula brevi tantum penetrans. Oosporae pleroticae, cuticulis levibus, unicam globulam et corpus prolatum ellipsoidale vel complanatum habentes; germinatio non visa.[2]

Pythium hypogynum exhibits similarities to *P. rostratum* from which it may be distinguished by the character of the antheridium, the predominance of acrogenous sporangia and its strictly terminal oogonia. The antheridial character also serves to separate the species from *P. iwayamai* which has either mono- or diclinous, never hypogynous antheridia.

Pythium hypogynum represents one of a series of species with analagous or related types of antheridia, such as found in *P. rostratum*, *P. proliferum*, *P. pulchrum*, *P. paroecandrum*, *P. ultimum*, and perhaps others. Though the antheridia of these several species are similar, the species remain quite distinct and in some instances not at all closely related. It is interesting to consider the possible origin and evolution of the types embraced in this group of species. Assuming the premise of evolutionary advancement through reduction and simplification, species such as *P. hypogynum* and *P. pulchrum* would be derived from organisms such as *P. ultimum* and *P. paroecandrum*, cases in which the sessile, monoclinous antheridium originating immediately

[2] Thanks are extended to Dr. H. W. Rickett for preparation of the Latin diagnosis.

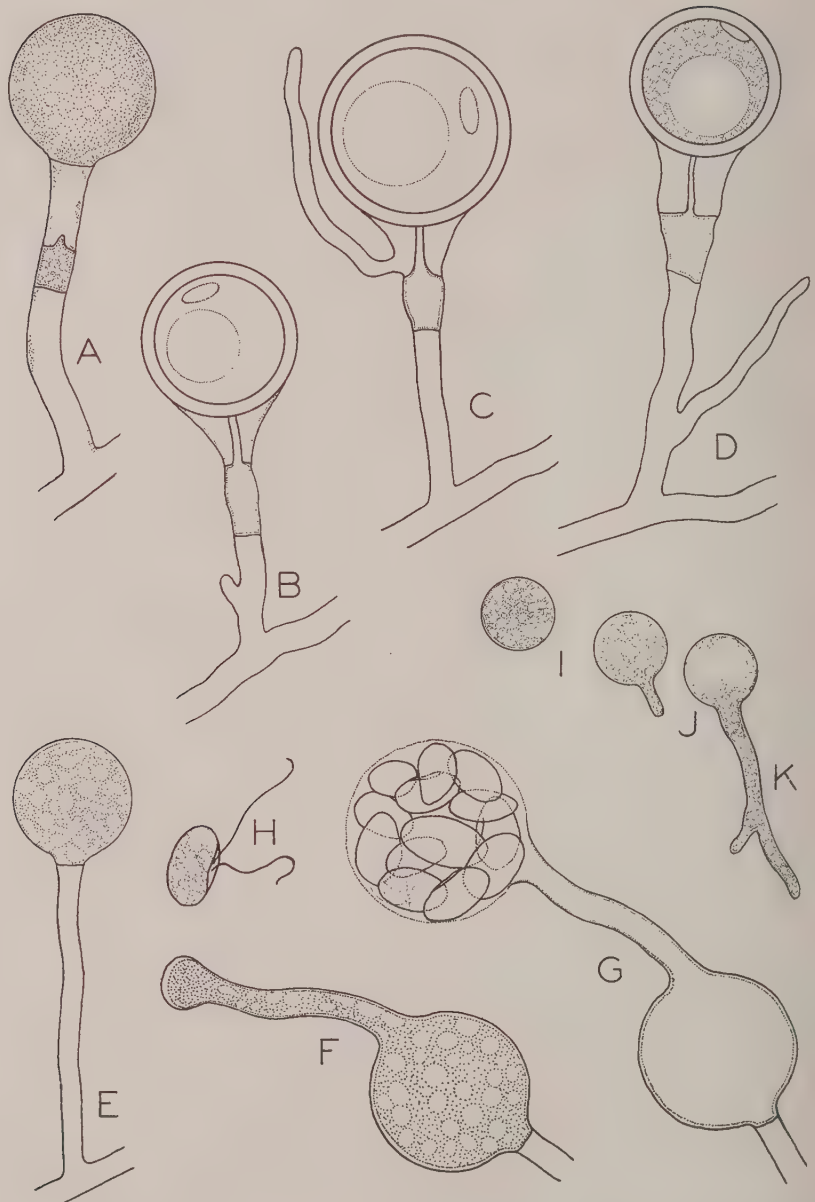

FIG. 5. *Pythium hypogynum*. *A–D*, Sexual apparatus. *A*, Unfertilized oogonium with differentiated periplasm with hypogynous antheridium forming a fertilization tube. *B–D*, mature oospores with empty antheridial cell. *E–K*, Asexual apparatus. *E*, Typical sporangium. *F*, *G*, Development of evacuation tube and vesicle containing zoospores. *H*, active zoospore. *I–K*, Three phases of zoospore germination.

adjacent to the oogonium and frequently not delimited from the oogonial stalk by a septum, has been further reduced to a mere lateral protuberance or hypogynal cell. *P. rostratum* and *P. proliferum* can be considered as intermediate types, either species showing partial reduction of the antheridium or complete reduction to the hypogynal cell; both of these extremes and their consequent intermediates are frequently encountered in a single isolate of either species. In fact, a morphologically distinguishable antheridium is often unidentifiable in *P. proliferum*. On rare occasion this absence of a visible antheridium has been observed in *P. hypogynum;* perhaps this condition reflects relationship to species completely lacking antheridia, such as *P. anandrum*, representing an additional advancement in evolutionary development. In several instances in which the antheridium was lacking in *P. hypogynum* the writer was able to demonstrate the migration of a single, moderately sized nucleus in the oogonial stalk upwards toward the oogonial cavity; this movement originated in the region where the antheridial cell is normally located. Subsequently an oospore developed. Whether this phenomenon occurs in all instances in apandrous oospore development is questionable. In any event it may account for fertilization of oogonia normally fecundated by functional antheridia which are upon occasion lacking. This observation certainly should be extended in the study of other species of this genus and may suggest the necessity of further cytological investigations in related genera and opening the question of fertilization in apandrous species and parthenogenesis in the fungi. Parthenogenesis in certain species of *Pythium* may be quite lacking, being so named for lack of cytological information.

The possible evolutionary trend indicated above solely on the basis of certain antheridial characteristics is not necessarily suggested when the asexual stage is considered. Sporangia of *Pythium ultimum* indicate the reverse relationship, these bodies having lost their ability to produce zoospores, germinating by means of germ tubes; the sporangia of *P. hypogynum* and *P. pulchrum* commonly germinate by the production of zoospores, a process generally accepted as more primitive. Whether or not a developmental trend has been established either through the antheridial or sporangial habits, a certain analogy exists among species possessing the antheridial types discussed.

The growth habit of *Pythium hypogynum* is radiate while that of *P. rostratum* is rosette. The temperature-growth responses of the two species are likewise dissimilar; the cardinal temperatures for *P. hypogynum* are 1°, 31° to 34°, and 37° C, while those for *P. rostratum* are 4°, 22° to 25°, and 34° C.

This species has been observed on *Heuchera hispida* Pursh. and *Hordeum vulgare* L. in the United States.

30. PYTHIUM ROSTRATUM Butler, Mem. Dept. Agr. India Bot. 1^5: 1–160. 1907.

Pythium diameson Sideris, Mycologia **24**: 14–61. 1932.

Hyphae often large, measuring up to 6 to 8 μ in diameter. Sporangia are spherical to oval, terminal or intercalary, measuring 23 to 34 μ, average 28 μ, in diameter, usually appearing before sexual reproductive bodies; zoospores few to 40, 8 to 11 μ, average 9.6 μ, in diameter at encystment, formed in a vesicle arising from a large, stout evacuation tube usually equal to the diameter of the sporangium, frequently of lateral origin. Oogonia spherical to subspherical, typically intercalary, occasionally terminal measuring 13 to 29.4 μ, average 21 μ, in diameter. Antheridia typically monoclinous, infrequently hypogynal, single, rarely 2 per oogonium, the antheridial cell often extremely short, reduced to a lateral swelling immediately adjacent to the oogonium, then 2 to 5 μ long and 3 to 5 μ wide, or strongly crook-necked, in either case arising from a cell cut off immediately below the oogonium, the antheridial cell sessile and not otherwise delimited, the whole forming the antheridium. Oospore plerotic, single, with a moderately thickened wall, measuring 12 to 27 μ, average 20 μ, in diameter; germination not observed.

Originally described as saprophytic in garden soil, France.

The most distinctive characteristic of *Pythium rostratum* is the antheridium; this readily distinguishes the species from its congeners *P. conidiophorum*, *P. hypogynum*, and *P. iwayamai*. *P. rostratum* is more closely related to *P. hypogynum* than to any other species, though differing from it not only in antheridia but also in the position of the oogonia which are principally intercalary in *P. rostratum* and acrogenous in *P. hypogynum*.

Sideris described *Pythium diameson* and *P. plerosporon* as new species. *P. diameson* is considered by the writer to be synonymous with *P. rostratum*. Until additional cultures of *P. plerosporon* are available for study, it seems advisable to retain this species as of doubtful validity and possibly as synonymous with *P. rostratum*.

The sporangia of *Pythium diameson* compare favorably with those of *P. rostratum*, being both acrogenous and intercalary, spherical to subspherical, though Sideris' measurements are somewhat smaller, 15 to 20 μ in diameter compared with 23 to 34 μ in diameter for *P. rostratum*. Measurements of sporangia of *P. diameson* made by the writer are slightly larger, 14.1 to 28.3 μ in diameter; similar differences were found in the size of the oogonia, Sideris reporting 15 to 17 μ in diameter, the writer 12.2 to 29.3 μ in diameter. Although the oogonia of *P. diameson* are reportedly mostly acrogenous, large numbers of intercalary ones can be found. The antheridia of both species are similar, perhaps more frequently longer in *P. diameson* than in *P. rostratum*, nevertheless exclusively monoclinous, usually sessile and oriented as those in *P. rostratum*. The oospores of both species are plerotic and fairly thick walled. The growth habits and temperature-growth responses of the two species are identical.

Pythium rostratum and *P. hypogynum* may be further distinguished by their mycelial type of growth and temperature responses.

Pythium rostratum is listed from the following substrates:

Ananas comosus Merr. HAWAII: Sideris and Paxton (1931); Sideris (1932); Parris (1940)
Antirrhinum majus L. UNITED STATES: Author.

Avena sativa L. UNITED STATES: Author.
Cajanus indicus Spreng. HAWAII: Sideris (1932); Parris (1940).
Canavalia ensiformis DC. HAWAII: Sideris (1932); Parris (1940).
Citrus aurantium L. UNITED STATES: Wager (1942b).
C. limonia Osbeck. UNITED STATES: Wager (1942b).
Erica regerminans L. UNITED STATES: Author.
Fuchsia sp. UNITED STATES: Author.
Hordeum vulgare L. UNITED STATES: Author.
Ipomoea batatas Lam. HAWAII: Sideris (1932); Parris (1940).
Lactuca sativa L. UNITED STATES: Author.
Lathyrus odoratus L. UNITED STATES: Author.
Lupinus angustifolius L. GERMANY: Schultz (1939).
Lupinus arboreus Sims. UNITED STATES: Author.
Medicago sativa L. UNITED STATES: Buchholtz and Meredith (1938); Author.
Nemophila menziesii H. and A. UNITED STATES: Author.
Oryza sativa L. UNITED STATES: Author.
Pennisetum barbinode.[3] HAWAII: Sideris (1932); Parris (1940).
Persea americana Mill. UNITED STATES: Author.
Phaseolus aureus Roxb. UNITED STATES: Author.
P. vulgaris L. UNITED STATES: Author.
Saccharum officinarum L. HAWAII: Sideris (1932); Parris (1940).
Soil. FRANCE: Butler (1907). UNITED STATES: Meredith (1938, 1940); Author.
Solanum tuberosum L. HAWAII: Sideris (1932); Parris (1940).
Spinacea oleracea L. UNITED STATES: Author.
Triticum aestivum L. UNITED STATES: Author.
Vicia faba L. HAWAII: Sideris (1932); Parris (1940). UNITED STATES: Author.
Zea mays L. HAWAII: Sideris (1932); Parris (1940).

31. PYTHIUM IWAYAMAI Ito, Trans. Sapporo Nat. Hist. Soc. **14**: 11–33. 1935.

Pythium sp. Iwayama, Toyama Agr. Expt. Sta. Publ. 1933.

Hyphae intra- and extramatrical, hyaline to olive-yellow, branched, measuring 2.9 to 8.9 μ, average 6.6 μ, in diameter. Sporangia spherical to prolate ellipsoidal, ovoid or citriform, acrogenous, wall thin and light olive-yellow, measuring 28 to 48 μ long by 44 μ wide; zoospores 8 to 12, when encysted measuring 9 to 15 μ in diameter. Chlamydospores intercalary, ellipsoidal, pale olive in color, 36 to 48 μ long and 24 μ wide with a more or less thick wall. Oogonia terminal or intercalary, spherical, smooth. Antheridia monoclinous or diclinous, usually single, sometimes two, clavate. Oospores plerotic, pale olive-yellow in color, measuring 19 to 24 μ in diameter.

Originally described as parasitic on *Hordeum vulgare* L. and *Triticum aestivum* L., Japan.

Cultures of this fungus were not available to study and inasmuch as no other reports of the species exist at present, the discussion is confined to the translated description given above, apparently prepared from Iwayama's original report.

The usually elliptical or limoniform sporangia are somewhat larger than those of any of its congeners, *Pythium conidiophorum*, *P. hypogynum*, and *P. rostratum*, about 40 μ in diameter compared with 14 μ, 23 μ and 28 μ in diameter, respectively.

Pythium iwayamai is the only species of the group with nonproliferous sporangia and plerotic oospores which has stalked antheridia that are either monoclinous or diclinous and never hypogynous.

[3] This probably stands for *Pennisetum purpurascens* var. *barbinode* Kuntze (*Panicum barbinode* Trin.).

Iwayama described a rot of cereals occurring under snow, calling it the snow-rot disease. An unidentified species of *Pythium* was isolated from the material and proven pathogenic by inoculation. The fungus was described but not given a specific name until Ito reported it to be a new species in 1935. Iwayama states that the optimum temperature for growth is between 15° and 18° C.

The fungus is unknown from any other hosts than those from which it was originally described. In Ito's description it is stated to be limited to graminicolous hosts, ". . . necnon implantis plurimorum speciorum gramineorum," though no data are presented to substantiate the statement.

32. PYTHIUM PROLIFERUM de Bary, Jahr. Wiss. Bot. **2**: 169–192. 1860.

Hyphae freely branched and well developed on most culture media, measuring 2 to 5 μ in diameter. Sporangia acrogenous, spherical to ovoid, measuring 24 to 36.6 μ in diameter, proliferous, the secondary and tertiary sporangia formed within the walls of the primary ones; zoospores 3 to 40, reniform and laterally biciliate, formed in a vesicle borne on a short, stout evacuation tube, zoospores measuring 9 to 16 μ in diameter upon encystment. Oogonia spherical, smooth or with a short apical papilla, terminal or intercalary, frequently catenulate, measuring 15 to 28 μ in diameter. Antheridia hypogynous, monoclinous or diclinous, 1 to 3 per oogonium, usually single and hypogynous, when mono- or diclinous, either sessile or stalked, only slightly inflated, clavate, making moderate apical contact with the oogonial wall. Oospores aplerotic, thick-walled, measuring 14 to 24 μ in diameter, containing a single reserve globule and refringent body; germination not observed.

Originally described from insect cadavers in Germany.

De Bary originally described this species from the asexual stage only; it was not until later that he reported the sexual phase (1881a, 1881b).

This species has received considerable attention from various mycologists, probably because it is easily isolated and readily produces proliferous sporangia. Butler (1907), Crooks (1937), Dissmann (1927) and Ward (1883) all present similar accounts of the fungus. Büsgen (1882) includes a discussion of this species in his study of the development of the sporangium.

The sporangium is usually papillate with the evacuation tube arising from the papilla. The secondary or tertiary sporangia are usually formed within the primary but sometimes beyond it. Occasionally sporangia may germinate by the production of germ tubes rather than zoospores.

Although the oogonium does not exhibit any unique peculiarities, the oospore differs from that of the other proliferous sporangial species, *Pythium polytylum*, *P. helicoides*, *P. oedochilum*, and *P. paligenes*, in containing a single reserve globule and refringent body whereas the others contain several. The number of reserve globules contained in an oospore is considered a specific feature in the segregation and identification of these species. This feature, together with the occurrence of a hypogynal antheridium serves to distinguish *P. proliferum* from its allies.

Pythium proliferum has been isolated from *Fragaria chiloensis* Duchesne in Scotland by Wardlaw (1927); from *Gossypium* sp. in the Anglo-Egyptian Sudan by Andrews and Clouston (1939); from insect cadavers in England by Ward (1883), in France by Butler (1907), in Germany by de Bary (1881a) and Schroeter (1889), in India by Butler (1907), Butler and Bisby (1931) and by Sydow and Butler (1907); from *Medicago sativa* L. in the United States by the author; from *Nymphaea* sp. and *Nuphar* sp. in Denmark by Petersen (1909, 1910); *Nymphaea candida* Presl. in Bohemia by Dissmann (1927); *Ricinus communis* L. seeds in India by Butler and Bisby (1931); soil in the United States by Harvey (1927), Höhnk (1933), Matthews (1931), Raper (1928) and the author; vegetable debris in France and India by Butler (1907) and in the United States by the author; water in Australia by Crooks (1937) and in the United States by Matthews (1931). A fungus which may be this species has been isolated from *Bromus inermis* Leyss. and *B. tectorum* L. by Fischer *et al.* (1942) in the United States.

33. Pythium marsipium Drechsler, Phytopathology, 31: 478–507. 1941.

Hyphae branched, measuring 2 to 7.5 μ in diameter. Sporangia spherical or asymmetrically utriform, papillate, broadly rounded at one end and skewly beaked at the other, proliferous, generally by production of the secondary sporangium within the primary, when subspherical measuring 20 to 70 μ in diameter, largely intercalary in broad hyphae but sometimes acrogenous, when utriform measuring 25 to 70 μ in length by 20 to 45 μ in width, largely acrogenous on sporangiophores 20 to 100 μ long and 3 to 4 μ wide with the long axis of the sporangium transverse or oblique to the supporting stalk; zoospores sometimes produced in a vesicle sessile on the papilla, more frequently the vesicle is formed at the apex of an evacuation tube 2 to 8 μ wide and up to 100 μ in length which may or may not arise from the papilla, zoospores reniform, laterally biciliate from the longitudinal groove, from 2 to 125 in number, measuring 9 to 12 μ in diameter when encysted. Oogonia subspherical, measuring 23 to 29 μ, average 30.9 μ, in diameter, acrogenous, subterminal, mostly intercalary, infrequently catenulate. Antheridia diclinous, 1 to 4 per oogonium, usually 1 to 3, irregularly expanded, 10 to 20 μ in length by 8 to 12 μ in width, broad oogonial contact with conspicuous fertilization tube. Oospores aplerotic, subspherical, measuring 19 to 33 μ, average 26.2 μ, in diameter, wall moderately thick, 1.3 to 2.8 μ, average 1.95 μ, containing a single reserve globule and refringent body.

Occurring in decaying leaves of *Nymphaea tuberosa* Paine, in the United States.

Cultures of this newly described species were not available for observation.

The sporangia resemble those found in *Pythiogeton* in being utriform, the long axis generally attached transversely or obliquely to the sporangiophore rather than parallel to it. The resemblance to *Pythiogeton* is only superficial, the organism resembling other *Pythium* species in all other respects.

Pythium marsipium should prove easily distinguishable from its congeners exhibiting proliferous sporangia and aplerotic oospores. *P. nagaii* differs from

this group in possessing a thin-walled oospore. *P. helicoides*, *P. oedochilum*, *P. palingenes*, and *P. polytylum* all differ from *P. marsipium* in their plurality of reserve globules and refringent bodies in their oospores; a single reserve globule and refringent body is present in *P. marsipium*. Drechsler (1941) suggests the term unitary for oospores of this latter type. *P. proliferum*, the only other species in this group possessing unitary oospores with an inspissate wall, exhibits sporangia and antheridia of quite different appearance. The utriform sporangia of *P. marsipium* alone would serve to separate this species from all the congeners listed above, including *P. nagaii* and *P. proliferum*. Whereas the antheridia of *P. proliferum* are either monoclinous, diclinous or hypogynal, those of *P. marsipium* are typically diclinous, rarely monoclinous and never hypogynal. The antheridial cell of *P. marsipium* more closely resembles that of *P. dissotocum* than any other, being inflated, short, crooked, with a broad apex which is closely appressed to the oogonial wall, the longitudinal axis of the antheridium coincident with the radius of the oogonium. The mono- and diclinous antheridial cells of *P. proliferum* are not as broad and stout, usually crooked, more clavate and make moderate to narrow apical contact with the oogonial wall.

Pythium marsipium is at present known only from decayed leaves of *Nymphaea tuberosa* Paine, collected in Wisconsin, U. S. A.

34. PYTHIUM POLYTYLUM Drechsler, Jour. Wash. Acad. **20**: 398–418. 1930.

Hyphae measuring 1.9 to 8.0 μ; appressoria usually abundant, curved, swollen, clavate, 6 to 8 μ in diameter at the apex. Sporangia subspherical, usually 28 to 33 μ in diameter, exclusive of the papilla present during resting stage, typically acrogenous, though also intercalary, and laterally intercalary, proliferous; sometimes the apical sporangium assumes a lateral position by the resumption of growth of the supporting filament; zoospores 10 to 35, longitudinally grooved, reniform, laterally biciliate, upon encystment measuring 9.5 to 11.5 μ in diameter. Oogonia subspherical, sometimes irregularly so due to protruding toward antheridium, smooth- and thin-walled, acrogenous, sometimes lateral and sessile on parent hypha, measuring 26 to 40 μ, average 32.6 μ, in diameter. Antheridia typically diclinous, sometimes monoclinous, and then originating at least 60 μ below the oogonium, 1 to 4, mostly 1 or 2 per oogonium, lateral and sessile, but typically terminal on branches 5 to 80 μ, average 25 μ, long, antheridial stalk rarely exhibiting helicoid involvements, antheridial cells curved, elongate—cylindrical, frequently wavy in profile, 15 to 40 μ, average 30 μ long and 5 to 7.5 μ, average 6 μ, wide, the entire length usually intimately applied to the oogonium, the ferlization tube arising from the navel position. Oospores aplerotic, single, measuring 25 to 33 μ, average 28.8 μ, in diameter, with a wall 2.1 to 3.4 μ, average 2.6 μ, thick, containing 6 to 20 reserve globules and 4 to 8 or more refringent bodies; germination not observed.

Originally isolated from *Prunella vulgaris* L., in the United States.

A single isolation obtained by the writer from roots of spinach, *Spinacea oleracea* L., is referable to this species.

Pythium polytylum is one of four species having several characteristics in common, namely oospores containing several reserve globules, thick oospore walls, cylindrical, inflated antheridia, and papillate sporangia.

The morphological details of *Pythium polytylum* are adequately presented above.

Pythium polytylum is distinguished from its congeners, *P. helicoides*, *P. oedochilum*, and *P. palingenes* in possessing a spherical, papillate sporangium, whereas the other species have ovoid to obovoid papillate sporangia. The sporangia of *P. polytylum* are proliferous though they do not proliferate as readily as those of *P. palingenes* and *P. helicoides*.

The antheridia of *Pythium polytylum* are usually diclinous, the antheridial cell typically elongate, cylindrical and irregular in outline; the navel position of the fertilization tube is common to this species and *P. helicoides*, *P. oedochilum*, and *P. palingenes*. The antheridial stalk is rarely helicoid about the oogonial stalk, not as in *P. helicoides*. The antheridium, oogonium and oospore are of little value in segregating the species from related forms.

The fungus is known only from roots of *Prunella vulgaris* L. and *Spinacea oleracea* L. in the United States.

35. PYTHIUM HELICOIDES Drechsler, Jour. Wash. Acad. **20**: 398–418. 1930.

Hyphae measuring 4 to 9.5 μ in diameter, appressoria usually present, clavate, measuring 6 to 8 μ near the apex. Sporangia typically obovoid, sometimes subspherical, papillate, acrogenous, on long hyphae, often in racemose or cymoid arrangement, the sporangia sometimes lateral from prolongation of the supporting element, proliferous, measuring 9 to 40 μ, average 28 μ, in width, and 17 to 45 μ, average 31 μ, long, excluding the papilla which is about 4 μ long and 6 μ at the base; zoospores 2 to 40, longitudinally grooved, reniform, laterally biciliate, measuring 10 to 15 μ, average 12.3 μ, in diameter upon encystment, capable of repeated emergence. Oogonia subspherical, sometimes broadly protruding toward the antheridium, smooth-walled, typically acrogenous though often laterally sessile, measuring 26 to 40 μ, average 33 μ, in diameter. Antheridia diclinous, 1 to 4, occasionally 2 antheridia borne on a single branch, the antheridial cell elongated, curved, cylindrical, regular in contour, measuring 20 to 42 μ long and 6 to 9 μ wide, intimately applied to the oogonial wall and producing a fertilization tube from the navel position; a part of the antheridial branch or branches or a lateral prolongation of the branch wound about the oogonial stalk in 2 to 4 close helical turns. Oospores aplerotic, measuring 21 to 32 μ, average 27.5 μ, in diameter, provided with a thick wall measuring 2.5 to 3.2 μ, containing 6 to 20 reserve globules and 2 to 4 refringent bodies.

Originally described from *Phaseolus vulgaris* L. in the United States.

Four isolates of this fungus were obtained by the writer; these cultures were used as the basis for the following discussion.

The sporangia of *Pythium helicoides* are very similar to those of *P. oedochilum* and *P. palingenes* and only serve to distinguish this group of three species from *P. polytylum*.

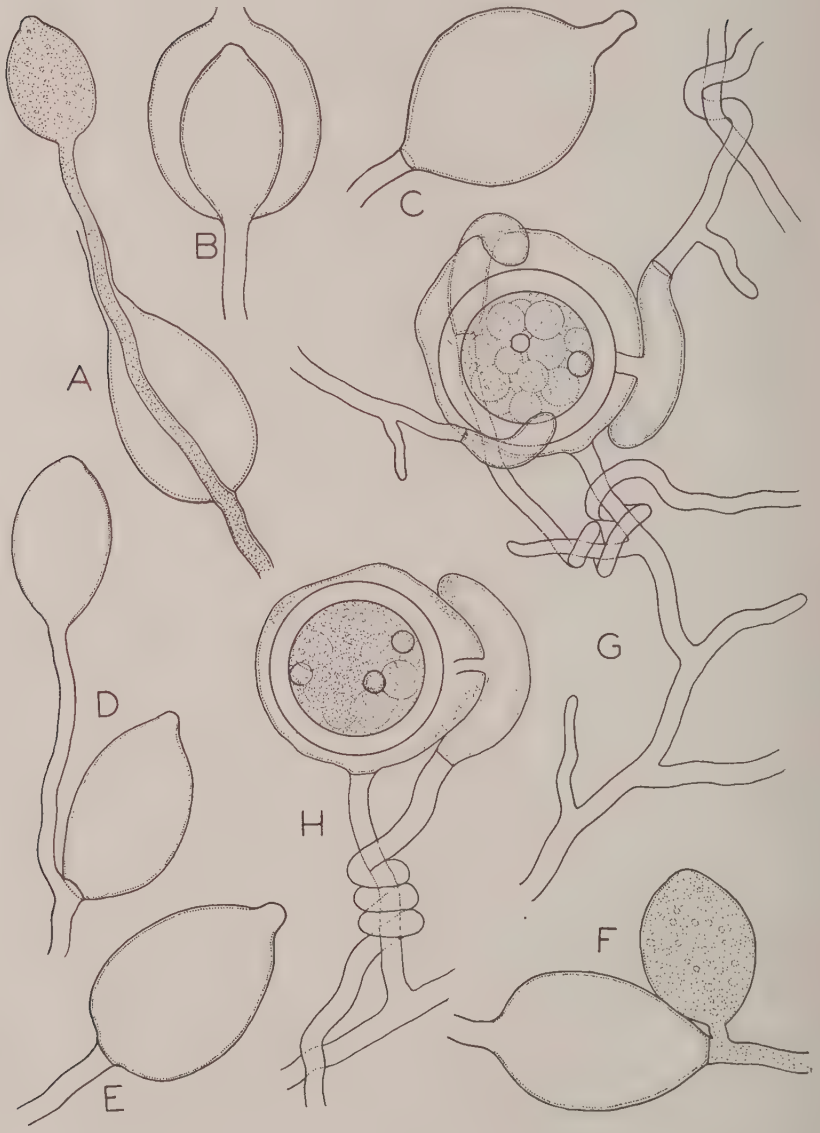

FIG. 6. *Pythium helicoides*. *A–F*, Sporangia. *A*, *B*, Two types of proliferation with production of secondary sporangia. *C*, Sporangium with normal papilla. *E*, Sporangium with elongated and distorted papilla. *D*, *F*, Production of secondary sporangia from the sporangiophore at the base of the primary sporangium. *G*, *H*, Sexual apparatus. Oospores with plural reserve globules and refringent bodies. Note the navel position of the antheridial fertilization tube.

Drechsler (1939) recently has given an account of *Pythium helicoides* which is supplementary to the original description of the species. He points out the similarity of the sexual stages of *P. helicoides*, *P. oedochilum*, *P. palingenes*, and *P. polytylum* but does not indicate the differences. The distinctive features by which this species may be identified, in the writer's opinion, are given below.

The antheridium of *Pythium helicoides* is like that of *P. volutum* in being regularly applied about the oogonial stalk in several helicoid turns. The antheridial cell is cylindrical, elongate, curved and regular in contour, the fertilization tube arising in a navel position. The regular, smooth and unfurrowed character of the antheridial cell distinguishes this species from *P. oedochilum* and *P. palingenes*. Although the coiling of the antheridial branch about the oogonial stalk is commonly observed in *P. helicoides*, it cannot be used as a valid taxonomic feature, for helicoidally disposed antheridial branches are occasionally observed in *P. oedochilum* and *P. palingenes*.

The repetitional emergence of zoospores reported in this species by Drechsler is also occasionally observed in *Pythium palingenes* and *P. aphanidermatum*.

The maximum temperature for mycelial development of *Pythium helicoides* is higher than that of *P. oedochilum;* temperature values for *P. palingenes* are lacking.

Pythium helicoides has been isolated from *Citrullus vulgaris* Schrad. by Drechsler (1939), from *Phaseolus vulgaris* L., by Drechsler (1930a) and the author, from *Pisum sativum* L. and *Spinacea oleracea* L. by the author, all in the United States.

36. PYTHIUM OEDOCHILUM Drechsler, Jour. Wash. Acad. Sci. **20**: 398–418. 1930.

Hyphae measuring 1.8 to 6.5 μ; appressoria sparingly produced as swollen, clavate, curved bodies measuring 5 to 7 μ at their apices. Sporangia ovoid to obovoid, subspherical, typically acrogenous, sometimes later in a lateral position due to continued growth of the sporangiophore, rarely intercalary, proliferous, smooth-walled, papillate, the papilla 6 to 8 μ long and same at base, sporangia measuring 17 to 42 μ, average 30 μ, in width and 25 to 48 μ, average 35 μ, in length; zoospores 10 to 35, longitudinally grooved, reniform and laterally biciliate, measuring 11 to 15 μ in diameter upon encystment. Oogonia subspherical, often with protruding wall toward antheridium, typically terminal, occasionally intercalary or laterally sessile, measuring 19 to 39 μ, average 31.5 μ, in diameter, provided with a stout, smooth wall. Antheridia usually diclinous, when monoclinous arising in excess of 40 μ from the oogonium, 1 to 4, usually 1 to 2, per oogonium, the curved, elongated, cylindrical, wavy contoured antheridial cells, usually borne terminally on branches not over 50 μ long; infrequently lateral and sessile, involvement of the oogonial stalk by the antheridium rare, though the oogonium is intimately attached by the antheridium usually over its entire length and producing a fertilization tube a bit forward of the navel position. Oospores aplerotic, single, measuring 16 to 34μ, average 28.1 μ, in diameter, with a

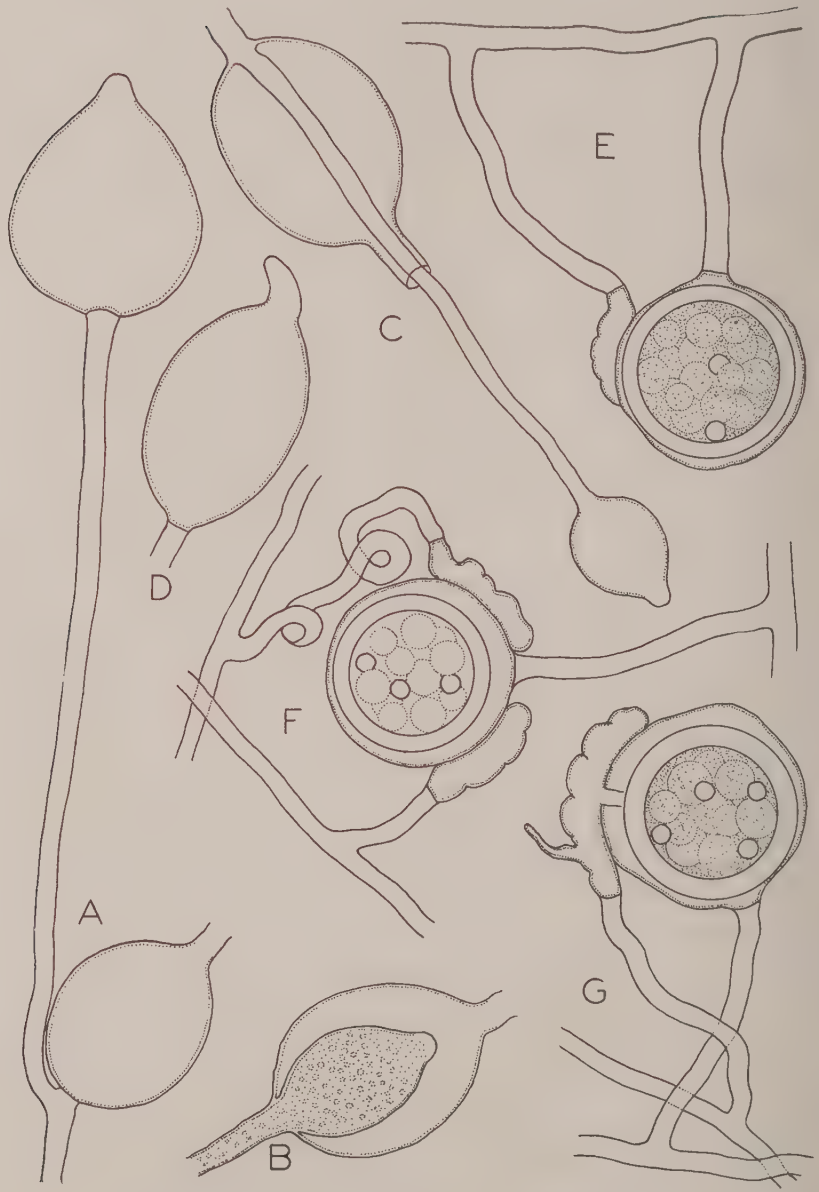

FIG. 7. *Pythium oedochilum*. *A–D*, Sporangia. *A*, Secondary sporangium borne on sporangiophore originating from base of primary sporangium. *B*, Secondary sporangium produced within the primary. *C*, Secondary sporangium produced outside the primary. *D*, Sporangium with skewed papilla. *E–G*, Sexual apparatus.

thick, smooth wall measuring 1.8 to 3.6 μ, average 2.5 μ, and containing 5 to 20 reserve globules and 3 to 20 refringent bodies.

Originally isolated from roots of *Dahlia* sp., United States.

Pythium oedochilum exhibits similarities to *P. polytylum*, *P. helicoides*, and *P. palingenes*, both in its asexual and sexual stages. The similarity is most marked in the structure of the oogonium, antheridium, and oospore. However, there are certain differences which permit segregation of the species. *P. oedochilum* differs from *P. polytylum* in having an ovoid to obovoid, papillate sporangium while that of *P. polytylum* is spherical and papillate. The elongate, cylindrical, curved antheridium of irregular, wavy contour of *P. oedochilum* is common to *P. polytylum* and *P. palingenes* but distinguishes *P. oedochilum* from *P. helicoides*, in which the antheridium is obviously regular and unfurrowed in outline. The oogonia of *P. oedochilum* are acrogenous and very rarely laterally sessile while those of *P. palingenes* are typically laterally and tangentially sessile, very rarely acrogenous. Although both *P. oedochilum* and *P. palingenes* have proliferous sporangia, they are tardily proliferous in the former and promptly in the latter.

The temperature values for mycelial development of *Pythium oedochilum* differ from those of *P. helicoides* and may be used as an adjunct to their differentiation: maximum temperature for growth of *P. oedochilum* is 40° C. and for *P. helicoides* is 43° C.

Pythium oedochilum has been isolated from *Bidens aristosa* (Michx.) Britton by Drechsler (1941), from *Citrullus vulgaris* Schrad. fruits by Drechsler (1939) and the author, from *Dahlia* sp., later said to be *D. rosea* Cav. (1941), by Drechsler (1930a), from roots of *Daphne odora* Thunb. and *Matthiola incana* R Br. by the author, all in the United States.

37. Pythium palingenes Drechsler, Jour. Wash. Acad. **20**: 398–418. 1930.

Hyphae measuring 2 to 7 μ in diameter; appressoria produced in moderate abundance, measuring 5.5 to 7.5 μ at the apex. Sporangia usually ovoid, sometimes subspherical, typically terminal, occasionally lateral due to prolongation of sporangiophore, rarely intercalary, proliferous, measuring 24 to 42 μ, average 33 μ, in length and 18 to 36 μ, average 29 μ, in width, excluding the sessile apical papilla approximately 6 μ wide at base and 4 μ long; zoospores 6 to 30, longitudinally grooved, laterally biciliate, reniform, measuring 11 to 17 μ, average 14 μ, in diameter upon encystment, exhibiting repetitional development. Oogonia subspherical, frequently protruding toward the antheridium, typically terminal on short lateral branches or sessile, laterally and tangentially intercalary, occasionally terminal on branches up to 75 μ or more, measuring 19 to 41, average 34 μ, in diameter. Antheridia typically diclinous, rarely monoclinous, 1 to 4, usually 2, per oogonium, the curved, elongated, cylindrical, irregularly contoured antheridial cells borne terminally on branches 5 to 50 μ long, sometimes lateral and sessile, often a portion of the antheridial branch coiled 2 or 3 times about the oogonial stalk, the antheridial cells measuring 20 to 28 μ long and 6 to 8 μ wide, usually closely applied their entire length to the oogonium, the fertilization tube originating forward of the navel position. Oospores aplerotic, measuring 18

to 37 μ, average 31.3 μ, in diameter, with a thick wall, 1.5 to 3.5 μ, average 2.6 μ and containing 5 to 30 reserve globules and 3 to 5 refringent bodies.

Originally described from roots of *Ambrosia trifida* L., in the United States.

No cultures of *Pythium palingenes* were observed by the writer, the following brief discussion being based on the original description and a subsequent paper by Drechsler (1941). *P. palingenes* is very closely related to *P. oedochilum* and its allies, *P. helicoides* and *P. polytylum*.

The ovoid to obovoid papillate sporangia of *Pythium palingenes* readily separates this species from *P. polytylum*, which has spherical papillate sporangia. The antheridial character, antheridial cell elongate, cylindrical, curved and irregular in outline, distinguishes *P. palingenes* from *P. helicoides* but not from *P. oedochilum*. The presence of predominantly acrogenous oogonia rather than laterally and tangentially intercalary oogonia segregates *P. oedochilum* from *P. palingenes*.

The numerous proliferous sporangia of *Pythium palingenes* are sharply contrasted with the only occasional proliferous sporangia of *P. oedochilum*. The repetitional emergence of zoospores without an intervening vegetative phase further distinguishes *P. palingenes* from *P. oedochilum*.

The presence of a single reserve globule in the oospore of *Pythium proliferum* in contrast with a plurality of reserve globules in *P. palingenes* makes confusion of the two species impossible. *P. palingenes* is distinguishable from *P. nagaii* in the character of the oogonial wall, inspissate in the former and not inspissate in the latter.

This species is only known through the two reports of Drechsler (1930a, 1941) stating its isolation from *Ambrosia trifida* L. in the United States.

38. Pythium nagaii Ito & Tokunaga, Jour. Fac. Agr. Hokkaido Imper. Univ. **32**: 201–233. 1933.

Hyphae measuring 1.5 to 4.0 μ in diameter. Sporangia spherical, ovoid or pyriform, proliferous, measuring 24 to 36 μ long by 20 to 26 μ wide; zoospores few to 25, formed in a spherical vesicle borne on short, apical evacuation tube, measuring 8.2 to 9.6 μ in diameter upon encystment, germinating by a tenuous hypha. Oogonia usually spherical, occasionally irregular in contour, measuring 14 to 22 μ in diameter. Antheridia monoclinous, single, delimited from the oogonial stalk by a septum, ovoid, round or clavate, more or less curved. Oospore aplerotic, typically single, spherical, measuring 12 to 19 μ in diameter, with a very thin oospore wall, approximately 0.8 μ thick containing a single reserve globule; germination not observed.

Originally described from seedlings of *Oryza sativa* L., Japan.

Two cultures of this fungus were observed by the writer, one from Baarn, the other from E. C. Tullis, Arkansas, and identified by V. D. Matthews. The cultures agreed with the delineation of the fungus by Ito and Tokunaga.

The only similarity of *Pythium nagaii* to *P. helicoides*, *P. marsipium*, *P. oedochilum*, *P. palingenes*, *P. polytylum*, and *P. proliferum* is the proliferous

nature of the sporangium and the aplerotic oospore. In the absence of the sexual apparatus positive identification cannot be assured although distinction between *P. nagaii* and all but *P. proliferum* is possible due to the difference in size of sporangia. The presence of utriform sporangia would preclude confusion with *P. marsipium*. As suggested by Drechsler (1941), instances in which proliferous sporangial species have been observed and referred to *P. proliferum* in the absence of any observations on the sexual phase may be of doubtful validity, inasmuch as there are a number of proliferous sporangial species very similar in the asexual stage but dissimilar in the sexual stage. The very thin oospore wall of *P. nagaii* immediately enables distinction from *P. proliferum* and all the other aplerotic oospore species with proliferous sporangia.

Though *Pythium nagaii* is morphologically separable from *P. helicoides* and *P. oedochilum*, the temperature-growth relation may be used as an adjunct to specific segregation.

This species is reported from *Oryza sativa* L. in Japan by Ito and Tokunaga, Darker (1940) and in the United States by Edson and Wood (1937).

39. Pythium anguillulae-aceti Sadebeck, Bot. Centralb. **29**: 318. 1887.

Hyphae fine. Sporangia, conidia and oogonia formed simultaneously. Sporangia rare, conidia numerous, produced in chains or in clusters of 4 to 5, spherical, about 6 μ in diameter, often deciduous; zoospores rarely formed. Oogonia numerous, very small, up to 6 μ in diameter. Oospores spherical, small, largest about 6 μ in diameter, germinating by germ tubes.

Parasitic on vinegar eelworm, *Anguillula aceti*, Germany.

This is a little known species, apparently not collected since its description.

The species may be identified by its extremely small apandrous oospores and oogonia. The conidia referred to in the description may be considered sporangia which germinate by the production of germ tubes rather than zoospores. The species is further distinguished by the catenulate arrangement of its sporangia.

40. Pythium pulchrum von Minden, Mykol. Untersuch. Ber. R. Falck **1**: 146–255. 1916.

Pythium epigynum Höhnk, Mycologia **24**: 489–507. 1932.

Hyphae measuring 1.5 to 7.5 μ in diameter. Sporangia spherical, elliptical or pyriform, terminal or intercalary, measuring 24 to 48 μ, average 38.2 μ, in diameter, occasionally catenulate, 2 to 4 in a series; zoospores few to 30 or more, formed in vesicle arising from an evacuation tube mesially or occasionally laterally situated, reniform, laterally biciliate, measuring 11 to 16 μ in diameter upon encystment. Oogonia more or less spherical, terminal or intercalary, sometimes 2 to 5 in a series, measuring 19.6 to 37.8 μ, average 28.3 μ, in diameter. Antheridia hypogynous, monoclinous or diclinous, 1 to 2 per oogonium, when monoclinous often sessile or a short lateral protrusion

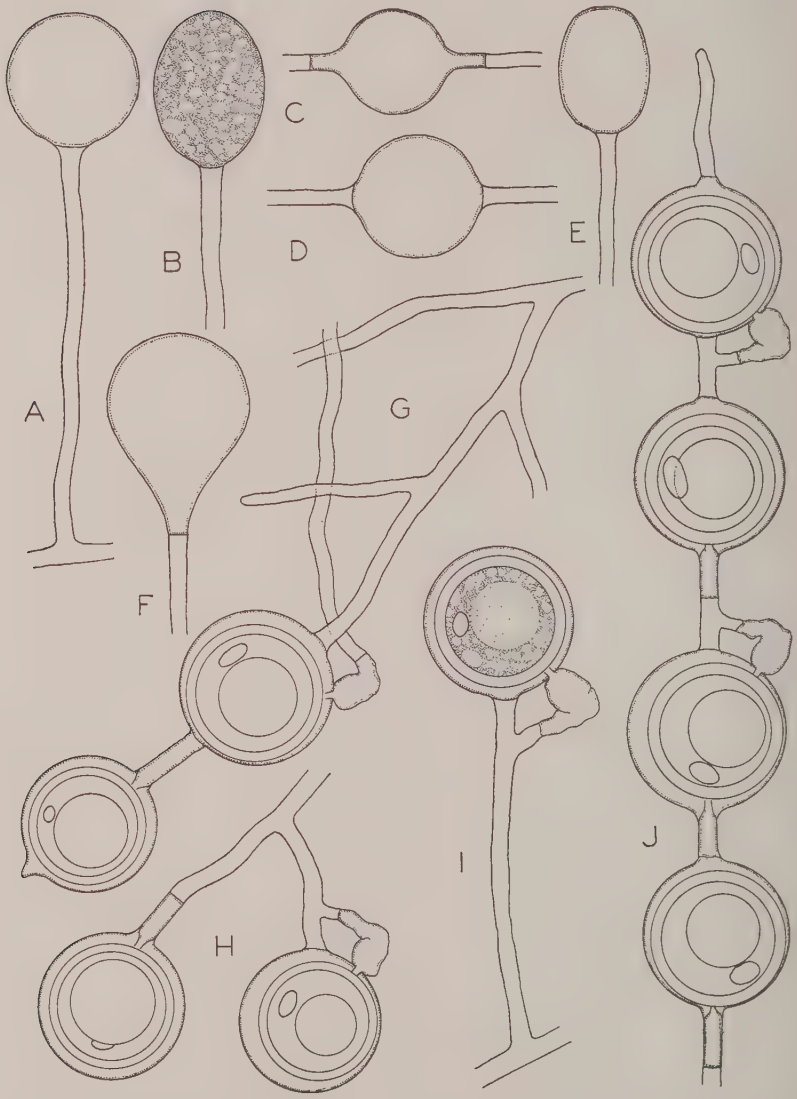

FIG. 8. *Pythium pulchrum*. *A–F*, Sporangia. *G–J*, Sexual apparatus. *G*, Two oogonia, one fertilized by a hypogynous antheridium, the other by a diclinous one. *J*, Catenulate oogonia with hypogynous and monoclinous antheridia.

originating immediately below the oogonium and delimited by a basal septum, then usually as long as it is broad, sometimes on a somewhat longer branch, the antheridial cell only slightly swollen, clavate, making moderate oogonial contact. Oospore aplerotic, single, measuring 13.8 to 31.1 μ, average 24.6 μ, in diameter, with a moderately thick wall, containing a single reserve globule and refringent body.

Originally described as saprophytic on ant eggs, Germany.

Pythium pulchrum is unique among non-proliferous sporangial types with aplerotic oospores in having a hypogynous antheridial cell. Von Minden reports that the species possesses monoclinous as well as hypogynous antheridia and that the hypogynous type is the more common. The observations of the writer are in agreement with those of von Minden.

Additional distinction is afforded *Pythium pulchrum* by its sporangia which are frequently arranged in chains of 2 to 5; no catenulate sporangia were observed in *P. polymorphon*, *P. ultimum*, *P. paroecandrum*, *P. splendens*, and *P. debaryanum*.

Pythium epigynum cannot be considered distinct from *P. pulchrum* despite the remarks of its author. The difference in the sizes of the sporangia, oogonia, and oospores of these two species are insufficiently different to permit specific segregation; both organisms have similarly shaped asexual and sexual bodies. The sporangia of these species are both borne in chains; both have aplerotic oospores. The absence of monoclinous or diclinous antheridia in *P. epigynum* cannot be used as a basis for separation from *P. pulchrum* for certain strains of *P. pulchrum* have been observed which failed to produce other than hypogynous antheridia.

Pythium pulchrum is known from animal debris in Germany by von Minden, from *Antirrhinum majus* L., *Callistephus chinensis* Nees and *Persea americana* Mill. by the author, from *Phaseolus vulgaris* L., *Pisum sativum* L., *Zea mays* L. and grass (unidentified) through inoculation by Höhnk (1932), from *Medicago sativa* L., by Buchholtz and Meredith (1938), from soil by Höhnk (1932, 1933), Matthews (1931) and Meredith (1938), all in the United States.

41. Pythium polymorphon Sideris, Mycologia **24**: 14–61. 1932.

Hyphae more or less uniform, measuring 4 to 8 μ in diameter. Sporangia spherical, subspherical or elliptical, terminal or intercalary, 20 to 40 μ, average 29.3 μ, in diameter, zoospores infrequently produced, the sporangia usually germinating by means of germ tubes. Oogonia spherical, terminal or intercalary, smooth to almost papillate, and thin-walled, measuring 13.2 to 29.8 μ (Sideris = 20 to 22 μ), average 22.1 μ, in diameter. Antheridia mono- or diclinous, 1 to 3 per oogonium, the antheridial stalk of variable length but typically falcate or sigmoid, the antheridial cell clavate, not greatly swollen nor curved, 8 to 12 μ long by 6 to 7.5 μ wide. Oospores aplerotic, single, measuring 10.3 to 25.1 μ (Sideris = 17 to 20 μ), average 18.2 μ, in diameter, with a smooth, unthickened wall.

Originally described as parasitic on *Ananas comosus* Merr., Hawaii.

Pythium polymorphon is one of the few species of *Pythium* which may be readily identified solely by the character of the antheridial branch, which is relatively long, originating either from the oogonial stalk or from a dissociated hypha, varying in length from approximately 50 to 180 μ, usually about 90 μ, and is falcate or sometimes sigmoid in shape. The antheridial cell is allantoid-clavate, the apex narrowly applied to the oogonium in the upper or lower equatorial plane.

The oogonium is similar to that of *Pythium debaryanum* in both size and shape. Occasionally, however, a few oogonia were observed which were of somewhat irregular contour, the irregularities more or less papillate; the latter type of oogonium resembles that infrequently observed in *P. irregulare*. Sideris reports that the oospores are sometimes echinulate. All observations made by the writer in an attempt to find echinulate oospores were unsuccessful. It is concluded that the echinulation mentioned by Sideris is more correctly referred to the oogonium than to the oospores.

In addition to the host from which the species was originally described, Sideris reports receiving a culture of the fungus from *Nicotiana tabacum* L. from the United States.

42. Pythium ultimum Trow, Ann. Bot. **15**: 269–312. 1901.

Hyphae long and slender, 1.7 to 6.5 μ, average 3.8 μ, in diameter, branched, septate only in old cultures, aerial growth luxuriant. Sporangia chiefly terminal and spherical, from 12 to 28 μ, average 20 μ, in diameter, occasionally intercalary and barrel-shaped, 14 to 17 μ, to 22.9 by 27.8 μ, in size, germinating only by germ tubes. Oogonia smooth, terminal, spherical, rarely intercalary, 19.6 to 22.9 μ, average 20.6 μ, in diameter. Antheridia usually 1 per oogonium, monoclinous from immediately below the oogonium, curved, sometimes 2 per oogonium, then often of diclinous origin and straight. Oospores aplerotic, single, spherical, 14.7 to 18.3 μ, average 16.3 μ, in diameter, with a smooth, thick wall, containing a single central reserve globule and refringent body.

Saprophytic on boiled potato tubers, house flies, cabbage leaves and other vegetable and animal substrata, England.

Despite the frequent occurrence of *Pythium ultimum* as a parasite on a large variety of hosts and the frequent isolation of this pathogen, few reports are available concerning the morphology of the species.

The report of van Luijk (1934a) is fairly typical of the treatment by many mycologists who prefer to consider *P. ultimum* a synonym of *P. debaryanum*. Van Luijk contends the differences between the two species are insufficient to warrant their retention as valid species. On the contrary Drechsler (1927) presents arguments in favor of the maintenance of the two binomials as distinct species. The writer concurs with Drechsler's opinion.

Pythium ultimum is distinguished from *P. debaryanum* by its typically monoclinous antheridia. The antheridium of *P. ultimum* originates immediately adjacent to the oogonium, is swollen, sharply curved upwards,

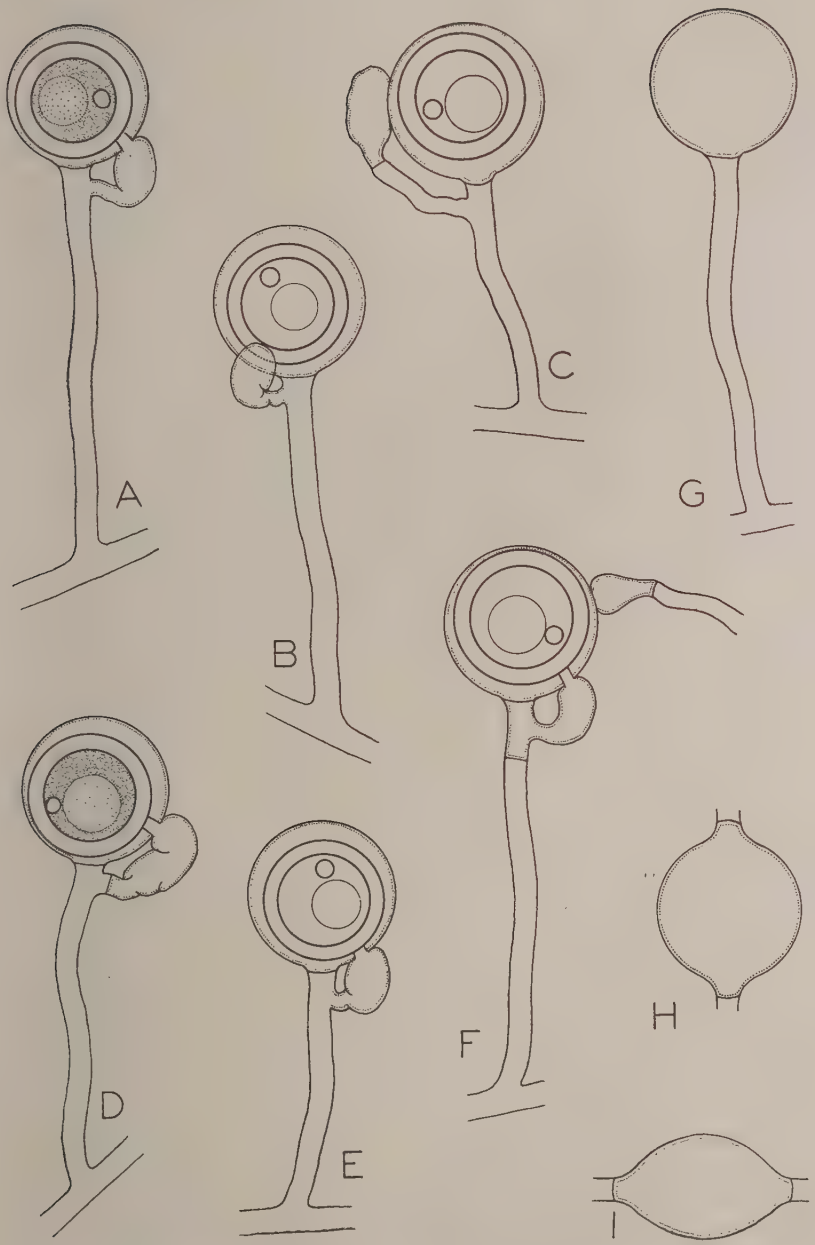

FIG. 9. *Pythium ultimum*. *A–F*, Sexual apparatus. *A–E*, Typical oogonia and oospores with monoclinous antheridium. *F*, Oogonium with both monoclinous and diclinous antheridia. *G–I*, Sporangia. *G*, Typical acrogenous sporangium. *H*, *I*, Intercalary sporangia.

making narrow apical contact with the basal portion of the oogonial wall, rarely delimited by a septum. The infrequent diclinous antheridia are similar to a variety of species and are not distinctive enough to be utilized in the identification of this species. The antheridium of *P. debaryanum*, although frequently monoclinous, never originates immediately adjacent to the oogonium and is never swollen or sharply upcurved. There is usually only a single antheridium in *P. ultimum*, while 2 to 6 are not uncommon in *P. debaryanum*, and the majority are diclinous.

There are also some differences in the oospores of *Pythium ultimum* and *P. debaryanum*. In *P. ultimum* the oospore wall is usually at least 2.0 μ thick, while the wall of *P. debaryanum* is somewhat thinner, not exceeding 1.5 μ in thickness. Drechsler (1927) reports that the reserve globule is smaller and that the refringent body is subspherical in *P. ultimum*, and that the reserve globule is larger and the refringent body oblate ellipsoidal in *P. debaryanum*. The absence of zoospores in *P. ultimum* may also distinguish the species, though no great degree of significance should be attached to this point.

Pythium ultimum may be segregated from *P. paroecandrum* on the basis of its antheridia. (Refer to *P. paroecandrum*.)

The growth habit and temperature values for *Pythium ultimum* are of no value in distinguishing this species from *P. debaryanum*.

Pythium ultimum is perhaps the most common member of the genus in the United States and frequently reported throughout the world; the following table presents the hosts and distribution of the species:

Achimines grandiflora DC. United States: Author.
Agropyron caninum (L.) Beauv. United States: Fischer *et al.* (1942).
A. cristatum (L.) Gaertn. United States: Fischer *et al.* (1942).
A. desertorum (Fisch.) Schult. United States: Fischer *et al.* (1942).
A. repens (L.) Beauv. United States: Fischer *et al.* (1942).
A. semicostatum (Steud.) Nees. United States: Sprague.
A. smithii Rydb. United States: Sprague.
Agrostis alba L. United States: Fischer *et al.* (1942).
Allium cepa L. United States: Tompkins *et al.* (1939).
Aloe variegata L. Union South Africa: Wager (1940). United States: Author.
Andropogon furcatus Muhl. United States: Fischer *et al.* (1942).
Antirrhinum majus L. United States: Middleton (1938); Nance (1939).
Apium graveolens L. var. *dulce* DC. United States: Alexander, Young and Kiger (1931); Author.
Arachis hypogea L. Union South Africa: Wager (1931, 1932a, 1940). United States: Wood and Nance (1938).
Arctotis stoechadifolia Berg. United States: Author.
Atropa belladonna L. United States: Middleton (1941a).
Azalea obtusum Planch. United States: Middleton.
Begonia lloydii (Hort. name). United States: Middleton (1938, 1942); Nance (1939).
B. semperflorens Link and Otto. United States: Maneval (1940); Middleton (1938); Middleton, Tucker and Tompkins (1938); Nance (1939).
B. tuberhybrida Voss. United States: Middleton (1938, 1942); Nance (1939).
Bellis perennis L. United States: Author.
Beta vulgaris L. United States: Poole (1934b); Wood and Nance (1938); Author.
B. vulgaris var. *crassa* Alef. Canada: Jones (1935).
B. vulgaris var. *macrorhiza*, Stev. Canada: Jones (1935). United States: Alexander, Young and Kiger (1931); Leach (1939); Author.

Boronia megastigma Ness. UNITED STATES: Author.
Bouteloua curtipendula (Michx.) Torr. UNITED STATES: Author.
Brassica campestris L. var. *napo-brassica*. UNITED STATES: Tompkins *et al.* (1939).
B. oleracea L. ENGLAND: Trow (1901). UNION SOUTH AFRICA: Wager (1932a, 1940). UNITED STATES: Drechsler (1925b, 1927); Harter and Whitney (1927a); Walker (1927); Author.
B. rapa L. UNITED STATES: Poole (1934b); Tompkins *et al.* (1939).
Bromus carinatus Hook and Arn. UNITED STATES: Sprague.
B. erectus Huds. UNITED STATES: Sprague.
B. inermis Leyss. UNITED STATES: Fischer *et al.* (1942).
Calceolaria crenatiflora Cav. UNITED STATES: Author.
Calendula officinalis L. UNITED STATES: Author.
Callistephus chinensis Nees. UNION SOUTH AFRICA: Wager (1931, 1932a, 1932c, 1940). UNITED STATES: Middleton (1938); Nance (1939).
Campanula medium L. UNITED STATES: Author.
Capsicum annuum L. UNITED STATES: Tompkins *et al.* (1939); Author.
Carludovica palmata Ruiz and Pav. PHILIPPINE ISLANDS: Roldan (1939).
Carica papaya L. AUSTRALIA: Simmonds (1937). RHODESIA: Hopkins (1939b). UNION SOUTH AFRICA: Doidge and Bottomley (1931); Wager (1931, 1932a, 1940). UNITED STATES: Author.
Chamaecyparis lawsoniana Parl. UNITED STATES: Author.
Cicer arietinum L. UNITED STATES: Middleton (1938); Nance (1939).
Citrullus vulgaris Schrad. UNITED STATES: Drechsler (1939); Middleton (1938); Nance (1939); Tompkins *et al.* (1939).
Citrus aurantium L. UNITED STATES: Author.
C. limonia Osbeck. UNITED STATES: Tompkins *et al.* (1939); Author.
C. sinensis Osbeck. UNION SOUTH AFRICA: Wager (1940). UNITED STATES: Tompkins *et al.* (1939); Author.
Clarkia elegans Dougl. RHODESIA: Hopkins (1939b).
Colchicum byzantium Ker-Gawl. ENGLAND: Moore (1940b).
C. speciosum Stev. var. *album*. ENGLAND: Moore (1940b).
Coleus sp. RHODESIA: Hopkins (1939b).
Cucumis melo L. UNITED STATES: Author.
C. melo var. *inodoratus* Naud. UNITED STATES: Tompkins *et al.* (1939).
C. melo var. *reticulatus* Naud. UNITED STATES: Tompkins *et al.* (1939).
Cucumis sativus L. UNITED STATES: Tompkins *et al.* (1939); Author.
Cucurbita maxima Duchesne. UNITED STATES: Tompkins *et al.* (1939).
C. pepo L. UNITED STATES: Tompkins *et al.* (1939).
C. pepo var. *condensa* Bailey. UNITED STATES: Middleton (1938); Nance (1939); Tompkins *et al.* (1939).
Cupressus sp. RHODESIA: Hopkins (1931, 1939b).
Cyphomandra betacea Sendt. UNITED STATES: Author.
Dahlia sp. UNION SOUTH AFRICA: Wager (1932a, 1940).
Daucus carota L. var. *sativa* DC. UNITED STATES: Tompkins *et al.* (1939); Author.
Delosperma sp. UNION SOUTH AFRICA: Wager (1940).
Delphinium sp. UNION SOUTH AFRICA: Wager (1940). UNITED STATES: Author.
D. ajacis L. UNITED STATES: Author.
D. cardinale Hook. UNITED STATES: Author.
D. consolida L. UNITED STATES: Author.
D. cultorum Voss. UNITED STATES: Author.
Dianthus barbatus L. UNITED STATES: Author.
D. caryophyllus L. UNITED STATES: Author.
D. plumarius L. UNION SOUTH AFRICA: Wager (1940). UNITED STATES: Author.
Dimorphotheca aurantiaca DC. UNITED STATES: Author.
Dinteranthus microspermis. UNION SOUTH AFRICA: Wager (1940).
Dioscorea batatas Decne. FRANCE: Foex, Dufrenoy and Labrousse (1931); Labrousse (1931b).
Duvalia parviflora. UNION SOUTH AFRICA: Wager (1940).
Echinochloa crus-galli (L.) Beauv. UNITED STATES: Sprague.
Elymus virginicus L. UNITED STATES: Sprague.
Euphorbia pulcherrima Willd. UNITED STATES: Middleton (1938); Nance (1939).

Fenestraria aurantiaca N. E. Brown. UNION SOUTH AFRICA: Wager (1940).
Fragaria chiloensis Duchesne. UNITED STATES: Author.
Fuchsia sp. UNITED STATES: Author.
Gaillardia aristata Pursh. UNITED STATES: Author.
Gilia sp. UNION SOUTH AFRICA: Wager (1940).
Gossypium sp. UNITED STATES: Arndt (1935).
Helipterum roseum Benth. UNITED STATES: Author.
Heuchera hispida Pursh. UNITED STATES: Author.
Hordeum vulgare L. UNITED STATES: Sprague; Author.
Ipomoea batatas Lam. UNION SOUTH AFRICA: Doidge and Bottomley (1931); Wager (1931, 1932a, 1940). UNITED STATES: Drechsler (1934); Edson and Wood (1936, 1937); Harter and Weimer (1929); Harter and Whitney (1927a, b); Nance (1939, 1940); Poole (1934a, b); Tompkins *et al.* (1939); Author.
Lactuca sativa L. UNITED STATES: Alexander, Young and Kiger (1931); Nance (1939, 1940); Owens (1939); Author.
Lathyrus odoratus L. UNION SOUTH AFRICA: Wager (1940). UNITED STATES: Guba (1936); Author.
Lepidium sativum L. ENGLAND: Trow (1901).
Lilium longiflorum Thunb. UNITED STATES: Author.
Lupinus sp. UNITED STATES: Author.
Lycopersicon esculentum Mill. ENGLAND: Vanterpool. NEW ZEALAND: Brien and Chamberlain (1936); Chamberlain and Brien (1937); Brien (1939). UNION SOUTH AFRICA: Wager (1940). UNITED STATES: Alexander, Young and Kiger (1931); Horsfall (1932a, b); Tompkins *et al.* (1939); Wilson and Tilford (1933); Author.
Malus sylvestris Mill. UNITED STATES: Tompkins *et al.* (1939).
Medicago sativa L. UNITED STATES: Buchholtz and Meredith (1938); Middleton (1938); Nance (1939).
Mesembryanthemum sp. UNION SOUTH AFRICA: Wager (1940).
Nasturtium sp. UNION SOUTH AFRICA: Wager (1932a, 1940).
Nicotiana biglovii S. Wats. var. *quadrivalvis*. UNITED STATES: Author.
N. tabacum L. RHODESIA: Hopkins (1939a). UNION SOUTH AFRICA: Wager (1940). UNITED STATES: Alexander, Young and Kiger (1931); Author.
N. trigonophylla Dun. UNITED STATES: Author.
Papaver nudicaule L. UNION SOUTH AFRICA: Doidge and Bottomley (1931); Wager (1931, 1932a, 1940). UNITED STATES: Author.
Pastinaca sativa L. UNITED STATES: Tompkins *et al.* (1939).
Pelargonium domesticum Bailey. UNITED STATES: Gill (1936).
P. graveolens L'Hér. UNITED STATES: Gill (1936).
P. hortorum Bailey. UNITED STATES: Gill (1936).
P. zonale L'Hér. CANADA: Bisby *et al.* (1938).
Persea americana Mill. UNITED STATES: Wager (1942a); Author.
Phaseolus aureus Roxb. UNITED STATES: Author.
P. vulgaris L. UNION SOUTH AFRICA: Wager (1932a, 1940). UNITED STATES: Harter and Whitney (1927a, 1927b); Middleton (1938); Nance (1939); Poole (1934b); Tompkins *et al.* (1939).
Phragmites communis Trin. UNITED STATES: Fischer *et al.* (1942).
Picea engelmanni Engelm. UNITED STATES: Rathbun-Gravatt (1931).
Pinus sp. PHILIPPINE ISLANDS: Roldan (1939). RHODESIA: Hopkins (1939a). UNION SOUTH AFRICA: Wager (1940).
P. aristata Engelm. UNITED STATES: Jackson (1940).
P. banksiana Lamb. UNITED STATES: Fischer (1941); Rathbun-Gravatt (1931).
P. resinosa Ait. UNITED STATES: Rathbun-Gravatt (1931); Author.
P. sylvestris L. UNITED STATES: Author.
Pisum sativum L. UNION SOUTH AFRICA: Wager (1932a, 1940). ENGLAND: Ogilvie, Croxall and Hickman (1940); Ogilvie and Hickman (1937); Baylis (1941). UNITED STATES: Parrot (1940); Author.
Poa ampla Merr. UNITED STATES: Fischer *et al.* (1942).
P. canbyi (Scribn.) Piper. UNITED STATES: Sprague.
P. secunda Presl. UNITED STATES: Fischer *et al.* (1942).

Primula malachoides Franch. UNITED STATES: Author.
P. obconica Hance. UNITED STATES: Author.
P. sinensis Lindl. UNITED STATES: Author.
Pseudotsuga taxifolia Britt. UNITED STATES: Jackson (1940); Weiss (1942).
Ranunculus asiaticus L. UNITED STATES: Tompkins and Middleton (1939, 1942).
Raphanus sativus L. UNITED STATES: Poole (1934b).
Rheum rhaponticum L. UNION SOUTH AFRICA: Wager (1931, 1932a, 1940). UNITED STATES: Middleton (1938, 1941b).
Ricinus communis L. UNITED STATES: Author.
Saccharum officinarum L. UNITED STATES: Rands (1930); Rands and Dopp (1938b); Stevenson and Rands (1938).
Saintpaulia ioanthe Wendl. UNITED STATES: Author.
Senecio cruentus DC. UNITED STATES: Author.
Sinningia speciosa Benth. and Hook. UNITED STATES: Author.
Soil. UNITED STATES: Meredith (1938, 1940).
Solanum melongena L. UNITED STATES: Tompkins *et al.* (1939).
S. tuberosum L. CANADA: Jones (1935). ENGLAND: Pethybridge and Smith (1930); Trow (1901). NEW ZEALAND: Brien (1939, 1940). UNION SOUTH AFRICA: Wager (1940). UNITED STATES: Poole (1934b); Tompkins *et al.* (1939); Author.
Sorghum vulgare Pers. UNITED STATES: Author.
Spinacea oleracea L. FRANCE: Dufrenoy (1931); Foex (1931, 1935); Foex, Dufrenoy and Labrousse (1931); Labrousse (1931a, 1931b, 1933). GERMANY: Fabel (1931). UNITED STATES: Nance (1940); Pirone *et al.* (1933); Author.
Stapelia sp. UNION SOUTH AFRICA: Wager (1940).
Streptocarpus sp. UNITED STATES: Author.
Striga lutea Lour. UNION SOUTH AFRICA: Wager (1931, 1940).
Tagetes erecta L. UNITED STATES: Author.
T. patula L. UNITED STATES: Middleton (1938); Nance (1939).
Tavaresia sp. UNION SOUTH AFRICA: Wager (1940).
Triticum aestivum L. UNITED STATES: Sprague; Author.
Tulipa gesneriana L. DENMARK: Moore and Buddin (1937). HOLLAND: Moore and Buddin (1937).
Ulmus americana L. UNITED STATES: Wright (1941).
U. pumila L. UNITED STATES: Author.
Vigna sinensis Endl. UNITED STATES: Middleton (1938); Nance (1939, 1940).
Viola tricolor L. UNITED STATES: Author.
Zea mays L. UNITED STATES: Sprague; Author.

Numerous other plants are reported as susceptible when grown in naturally infested soil inhabited by other soil fungi as well as by *Pythium ultimum;* for this reason these hosts are not listed. These hosts may be found by referring to the contributions of Haenseler (1935), Heuberger and Horsfall (1939), Horsfall (1932a, 1932b, 1934, 1935, 1938), Horsfall, Newhall and Guterman (1934), Kadow and Anderson (1937), Ogilvie and Hickman (1938), Pirone, Newhall, Stuart, Horsfall and Harrison (1933) and Seaver *et al.* (1932).

43. PYTHIUM PAROECANDRUM Drechsler, Jour. Wash. Acad. **20**: 398–418. 1930.

Hyphae measuring 2.7 to 9 μ in diameter; appressoria moderately abundant, apices curved and clavate, measuring 8 to 11 μ wide. Sporangia subspherical to prolate ellipsoidal, typically intercalary, occasionally terminal on either long or short laterals, when subspherical measuring 12 to 33 μ, average 22.8 μ in diameter, when ellipsoidal measuring from 16 μ long and 12 μ wide to 41 μ long and 36 μ wide, average 30.1 μ long and 23.0 μ wide;

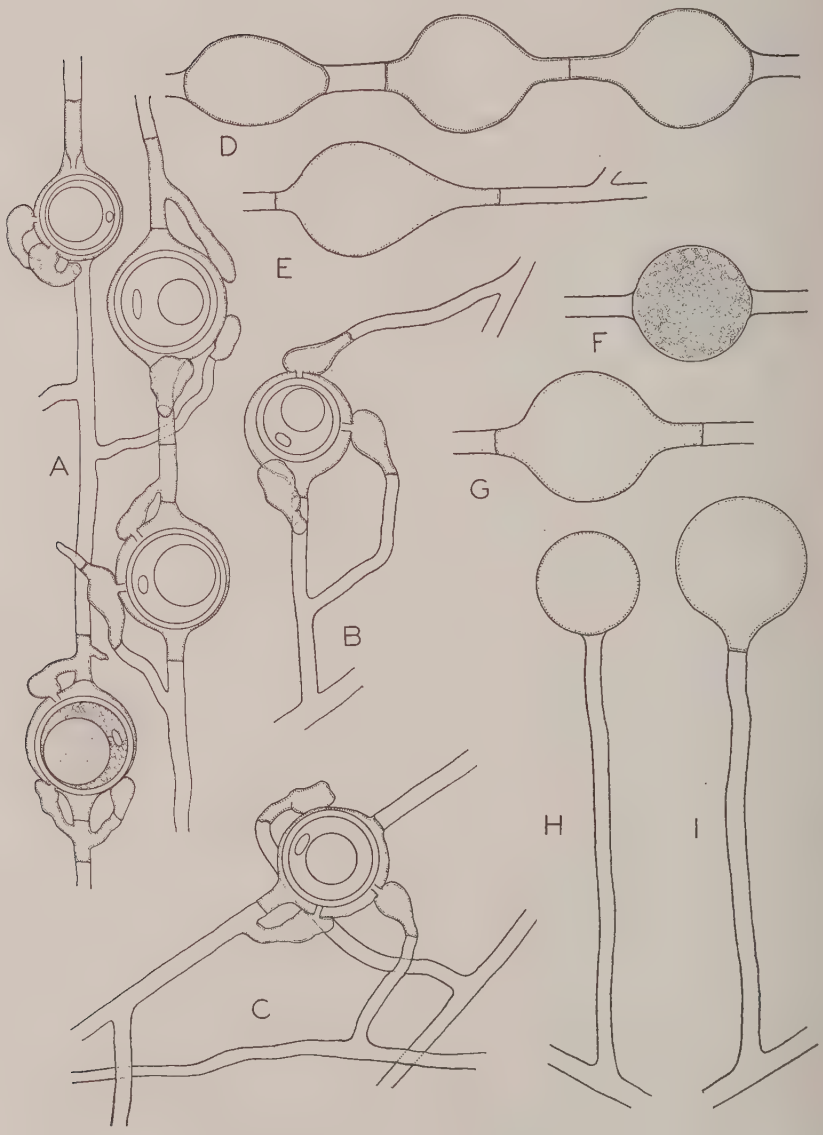

FIG. 10. *Pythium paroecandrum*. *A–C*, Sexual apparatus. *D–J*, Sporangia.

zoospores 3 to 25, biciliate, reniform, measuring 9 to 11 μ upon encystment. Oogonia subspherical, often including a portion of the supporting element on one end if acrogenous, both if intercalary, typically intercalary, occasionally acrogenous, measuring 11 to 28 μ, average 21.4 μ, in diameter, smooth- and thin-walled. Antheridia mono- and diclinous, 1 to 5 per oogonium, when monoclinous often undifferentiated and adjacent to oogonium, 7 to 15 μ long and 4 to 7 μ wide, sometimes swollen or together with a bulbous lateral outgrowth, sessile, and pouch-like or crook-necked, measuring 7 to 15 μ long and 6 to 8 μ wide, sometimes including an intercalary segment adjacent to the oogonium together with a proximal or distal cylindrical portion, sometimes two antheridia comprising one functional unit; when diclinous usually terminal, rarely intercalary, inflated, crook-necked, the antheridial cell 10 to 20 μ long and 6 to 8 μ wide. Oospores aplerotic, with a moderately thin wall, 1.1 to 1.5 μ, average 1.3 μ, thick, containing a single reserve globule and refringent body, oospore measuring 10 to 22 μ, average 18.3 μ, in diameter.

Originally described from roots of *Allium vineale* L., in the United States.

The asexual stage of *Pythium paroecandrum* is analogous with those of *P. debaryanum*, *P. irregulare*, *P. mamillatum*, and *P. ultimum*. The sexual stage of *P. paroecandrum* is, however, quite different from the species cited, with the exception of *P. ultimum*. Drechsler (1940) reports that the sexual stage of *P. paroecandrum* is similar to and yet distinct from that of *P. rostratum*, *P. pulchrum*, and *P. piperinum*. These species may be related, but the differences are sufficiently great to obviate any confusion among them. The oospore of *P. rostratum* is plerotic in contrast with the aplerotic condition in *P. paroecandrum*. The typical hypogynous antheridium readily separates *P. pulchrum* from the monoclinous antheridium of *P. paroecandrum*. *P. piperinum* is considered synonymous with *P. vexans* and exhibits antheridia strikingly different than those of *P. paroecandrum*.

Pythium paroecandrum and *P. ultimum* are quite similar and are most likely to be confused. The antheridium in both species is typically sessile, rarely stalked, and originates from the oogonial stalk immediately below the oogonium. Both species may have antheridia either mono- or diclinous but they are predominantly monoclinous. The typically single, monoclinous antheridium of *P. ultimum* is short, swollen, sharply hooked upward with the apex applied rather narrowly to the lower equatorial plane of the oogonium, usually in close proximity to the oogonial stalk. The antheridia of *P. paroecandrum* are also monoclinous but usually plural, with 2 to 5, usually 3, applied to an oogonium. The antheridial cell is of various shapes, usually either outwardly undifferentiated or somewhat saccate or swollen, neither uniformly inflated nor sharply hooked upwards and, though usually applied to the lower equatorial plane of the oogonium, not regularly placed in close proximity to the oogonial stalk.

The non-inspissate oospore wall of *Pythium paroecandrum* approximately 1.3 μ in thickness, further distinguishes this species from *P. ultimum* which has an inspissate wall about 2.2 μ thick.

Drechsler originally reported this species in the United States from *Allium vineale* L.; subsequently he reported it from *Impatiens pallida* Nutt. and *Sanguinaria canadensis* L. (1940); the author has obtained this fungus from *Aloe ciliaris* Haw. and *A. variegata* L., in the United States.

44. PYTHIUM SPLENDENS Braun, Jour. Agr. Res. **30**: 1043–1062. 1925.

Pythium splendens var. *hawaiianum* Sideris, Mycologia **24**: 14–63. 1932.

Hyphae measuring 3.5 to 9.2 μ, average 6.4 μ in diameter; falcate appressoria sometimes present. Sporangia spherical, acrogenous, smooth- and thin-walled, measuring 21.7 μ to 48.9 μ, average 36.2 μ, in diameter, usually dark in color on most nutrient substrates, usually displaying 1 to 2 light colored globules; zoospores rarely formed, germination usually through production of 1 to 6 germ tubes. Oogonia spherical, terminal, smooth- and thin-walled, measuring 25.5 to 34.7 μ, average 31.7 μ, in diameter. Antheridia mono- and diclinous, 1 to 8 per oogonium, clavate and crook-necked, making moderate oogonial contact. Oospores aplerotic, measuring 21.3 to 29.8 μ, average 26.6 μ, in diameter, supplied with a thick wall.

Originally described as parasitic on cuttings of *Pelargonium* sp., United States.

Pythium splendens is one of the few species of *Pythium* that may be identified solely on the basis of its sporangial characteristics. This is fortunate because the sexual stage is rarely produced in the standard culture media employed in this study.

The sporangia are spherical, acrogenous and large, measuring 22 to 49 μ, average 36 μ, in diameter, with a thin, smooth wall. The contents of the sporangium are characteristically dense, finely granular and dark in color, usually containing 1 to 3 small, hyaline globules. Sideris (1932) reports that the sporangia are spherical, subspherical and ellipsoid, mostly terminal and occasionally intercalary. Spherical sporangia were the only kind commonly observed by the writer and intercalary sporangia were seen only very rarely.

The writer concurs with Braun's description of the sexual stage and remarks concerning the temperature relations of the species.

A variety of *Pythium splendens* described by Sideris as *P. splendens* var. *hawaiianum* because it differed from the species ". . . in the stronger aerial mycelial development and the size of the conidia, which measure on an average of about 5 μ more in diameter" . . . is considered insufficiently distinct from the species to warrant its establishment as a variety. The temperature-growth response and growth habit are considered additional evidence of its synonymity with the species.

The hosts affected by *Pythium splendens* and their geographic distribution are given below:

Ananas comosus Merr. HAWAII: Parris (1940); Sideris (1932); Sideris and Paxton (1929, 1931).

Begonia sp. MALAYA: Sharples (1930). UNITED STATES: Braun (1925).

B. semperflorens Link and Otto. UNITED STATES: Maneval (1940); Middleton, Tucker and Tompkins (1938, 1942).

Cajanus cajan Millsp. HAWAII: Parris (1940); Sideris (1932).
Canavalia ensiformis DC. HAWAII: Parris (1940); Sideris (1932).
Carica papaya L. UNION SOUTH AFRICA: Wager (1931, 1932a, 1940).
Chrysanthemum sp. NETHERLANDS: Buisman (1927).
Citrus aurantium L. UNITED STATES: Author.
Coleus sp. UNITED STATES: Braun (1925); Author.
Cucumis sativus L. UNITED STATES: Braun (1925).
Geranium sp. NETHERLANDS: Buisman (1927).
Helianthus annuus L. HAWAII: Parris (1940; Sideris (1932).
Hordeum vulgare L. UNITED STATES: Author.
Ipomoea batatas Lam. HAWAII: Parris (1940); Sideris (1932). UNITED STATES: Harter and Whitney (1927b).
Linum usitatissimum L. NETHERLANDS: Diddens (1932).
Medicago sativa L. UNITED STATES: Buchholtz and Meredith (1938).
Nicotiana tabacum L. NETHERLANDS: Meurs (1928).
Pelargonium sp. UNITED STATES: Braun (1925).
P. zonale L'Hér. UNITED STATES: Dodge and Swift (1932).
Phaseolus aureus Roxb. HAWAII: Parris (1940); Sideris (1932).
P. vulgaris L. UNITED STATES: Harter and Whitney (1927a).
Piper betle L. MALAYA: Thompson (1939).
Raphanus sativus L. UNITED STATES: Braun (1925).
Saccharum officinarum L. HAWAII: Parris (1940); Sideris (1932); Stevenson and Rands (1938).
Triticum aestivum L. HAWAII: Parris (1940); Sideris (1932).
Vicia faba L. HAWAII: Parris (1940); Sideris (1932).
Vigna sinensis Endl. HAWAII: Parris (1940); Sideris (1932).

45. PYTHIUM VEXANS de Bary, Jour. Bot. **14**: 105–126. 1876.

Pythium complectens Braun, Jour. Agr. Res. **29**: 399–419. 1924.
Pythium allantocladon Sideris, Mycologia **24**: 14–63. 1932.
Pythium ascophallon Sideris, l.c.
Pythium euthyhyphon Sideris, l.c.
Pythium polycladon Sideris, l.c.
Pythium piperinum Dastur, Proc. Indian Acad. Sci. **1**: 778–815. 1935.

Mycelium fine, branched, with the hyphae tapering at the tip. Sporangia terminal or intercalary, pyriform, ovoid, subspherical to spherical, 17 to 24 μ, average 21 μ, in diameter, usually germinating by germ tubes, more rarely by zoospores. Oogonia spherical, smooth usually terminal on short lateral branches, occasionally inserted on a broad base, varying from 15 to 28 μ, average about 22 μ, in diameter. Antheridia usually 1, rarely 2, monoclinous, rarely diclinous and never hypogynous. Oospores aplerotic, smooth measuring 11 to 23 μ, average about 19 μ, in diameter, germinating by germ tubes or zoospores.

Originally described as saprophytic on tubers of *Solanum tuberosum* L., Germany.

Pythium vexans is readily distinguished from its congeners possessing aplerotic oospores by its typically monoclinous, stalked antheridium which arises in close proximity to the oogonium and by the clavate, swollen antheridial cell with the apex bell-shaped and broadly applied, sometimes fused with the oogonial wall.

A number of species are considered by the writer to be synonymous with *Pythium vexans*. Drechsler (1938) recently indicated the possible synonymity

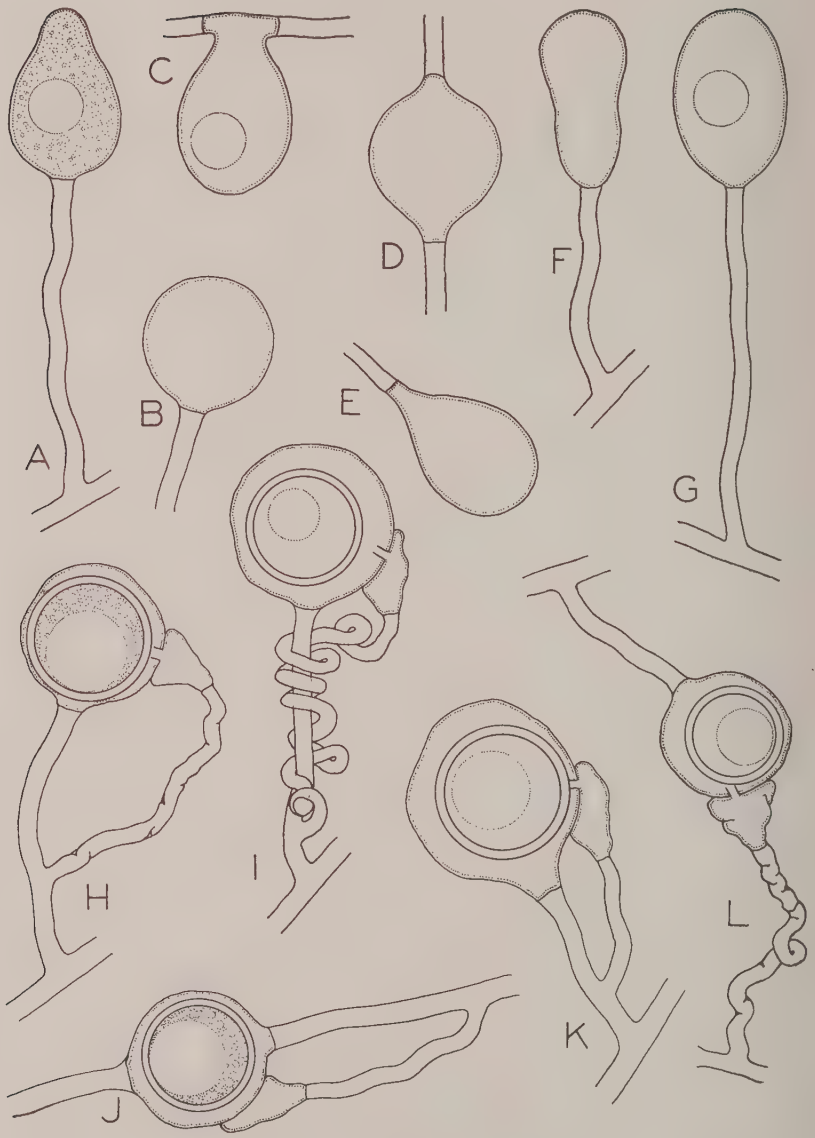

FIG. 11. *Pythium vexans*. *A–G*, Sporangia. *H–L*, Sexual apparatus. *H*, *J*, *K*, Typical structures. *I*, *L*, Structures with coiled or irregularly oriented antheridial branches occasionally observed.

of *P. complectens* and *P. vexans* but did not present evidence in support of his contention. His observation, however, is in agreement with that of the writer.

The species which are believed to be synonymous with *Pythium vexans* are *P. complectens*, *P. allantocladon*, *P. ascophallon*, *P. euthyhyphon*, *P. polycladon*, and *P. piperinum*. The oogonia and oospores of these species are similar in size, shape and position on the mycelium. A comparison of range and average diameters of their oogonia and oospores is presented below:

Name	*Oogonia* (μ)	*Oospores* (μ)
P. vexans	15–28 av. 22	11–23 av. 19
P. complectens	13–23 av. 19	11–21 av. 16
P. allantocladon	18–24 av. 21	10–20 av. 16
P. ascophallon	16–25 av. 21	12–18 av. 16
P. euthyhyphon	18–26 av. 20	12–21 av. 18
P. polycladon	av. 20	av. 20
P. piperinum	15–28 av. 21	13–20 av. 18

The sporangia of these strains are likewise indistinguishable. The antheridia of all except *Pythium piperinum* are similar and identical with those of *P. vexans*. The antheridium of *P. piperinum* resembles the type of antheridium described by Butler (1907) for his *P. vexans*. In this case the antheridial branch is multicellular and, though originating from the oogonial stalk, follows an irregular course. The supposedly multiple antheridia of *P. piperinum* are none other than the cells of the antheridial stalk which are intimately associated with the oogonium and were confused with the true antheridium.

The growth habits and temperature-growth relations of the several species considered synonymous with *Pythium vexans* are similar and are given here as additional evidence of their similarity to and synonymity with *P. vexans*.

Hosts for *Pythium vexans* are given below:

Agropyron inerme (Scribn. and Sm.) Rydb. UNITED STATES: Sprague.
A. smithii Rydb. UNITED STATES: Sprague.
Ananas comosus Merr. HAWAII: Parris (1940); Sideris (1932).
Antirrhinum majus L. UNITED STATES: Author.
Armeria sp. UNION SOUTH AFRICA: Wager (1940).
Arrhenatherum elatius (L.) Mert. and Koch. UNITED STATES: Sprague.
Avena sativa L. UNITED STATES: Sprague.
Bromus inermis Leyss. UNITED STATES: Sprague.
Carica papaya L. HAWAII: Parris (1940); Sideris (1932). UNION SOUTH AFRICA: Wager (1932a, 1940).
Citrus aurantium L. UNITED STATES: Wager (1942b); Author.
C. limonia Osbeck. UNITED STATES: Wager (1942b); Author.
Coleus sp. UNITED STATES: Braun (1924).
Delphinium ajacis L. UNITED STATES: Middleton (1938); Nance (1939).
Dianthus caryophyllus L. MALAYA: Thompson (1939). UNITED STATES: Author.

Durio zebethinus. Malaya: Thompson (1938, 1939).
Echinochloa crus-galli (L.) Beauv. United States: Sprague.
Elymus canadensis L. United States: Sprague.
E. glaucus Buckl. United States: Sprague.
Festuca ovina L. United States: Sprague.
Geum chiloense Balb. United States: Author.
Godetia grandiflora Lindl. United States: Author.
Hevea brasiliensis Muell. Indio-China: Anonymous (1941). Malaya: Thompson (1929).
Hordeum bulbosum L. United States: Sprague.
Linum usitatissimum L. Netherlands: Diddens (1932).
Lupinus albus L. Germany: Schultz (1939).
Matthiola incana R. Br. United States: Middleton (1938); Nance (1939).
Medicago sativa L. Germany: Schultz (1939).
Nemesia strumosa Benth. United States: Author.
Nicotiana tabacum L. (?) Java: Raciborski (1900).
Pelargonium sp. Uganda: Hansford (1938). United States: Braun (1924); Author.
Persea americana Mill. United States: Wager (1942a); Author.
Phragmites communis Trin. United States: Sprague.
Piper betle L. India: Dastur (1935).
P. longa India: Dastur (1935).
Poa nevadensis Vasey. United States: Sprague.
P. palustris L. United States: Sprague.
Ricinus communis L. Hawaii: Parris (1940); Sideris (1932).
Saccharum officinarum L. United States: Rands (1930); Rands and Dopp (1938b); Stevenson and Rands (1938).
Soil. England: Butler (1907). Ireland: Butler (1907). France: Butler (1907). United States: Meredith (1940); Author.
Solanum tuberosum L. Germany: de Bary (1876, 1881b); Frank (1881). India (?): Cunningham (1897).
Thea sinensis L. Malaya: Thompson (1936).

46. Pythium debaryanum Hesse, Inaugr. Dissert. Halle. 1874.

Pythium equiseti Sadebeck, Verhandl. Bot. Ver. Prov. Brand. **16**: 116–124. 1874.
Lucidium pythiodes Lohde, Tagebl. Versamm. Deuts. Naturf. Aerzte Breslau **47**: 203. 1874.
Pythium autumnale Sadebeck, Tagebl. Versamm. Deutsch. Naturf. Aerzte Breslau **49**: 100. 1876.
Artotrogus debaryanus Atkinson, Cornell Agr. Exp. Sta. Bull. **94**: 233–272. 1895.
Pythium haplomitrii Lilienfeld, Bull. Intern. Acad. Sci. Cracovie **1911**: 336. 1911.
Pythium debaryanum var. *pelargonii* Braun, Jour. Agr. Res. **30**: 1043–1062. 1925.
Pythium marchantiae Nicolas, Compt. Rend. Acad. Sci. **182**: 82–83. 1926.
Pythium fabae Cheney, Aust. Jour. Exper. Biol. Med. Sci. **10**: 143–155. 1932.
Pythium araiosporon Sideris, Mycologia **24**: 14–61. 1932.
Pythium cactacearum Preti, Riv. Pat. Veg. **26**: 331–353. 1936.

Hyphae branched, usually 5 μ in diameter, septate in old cultures. Sporangia spherical to oval, terminal or intercalary, 15 to 26 μ, average 19 μ, in diameter, germinating either by germ tubes or zoospores. Oogonia smooth, terminal or intercalary, usually spherical, 15 to 28 μ, average 21 μ, in diameter. Antheridia 1 to 6 per oogonium, monoclinous and diclinous, when monoclinous arising some distance below the oogonium, not adjacent to it. Oospores smooth, aplerotic, 12 to 20 μ, average 17 μ, in diameter, germinating by means of germ tubes.

Parasitic and saprophytic on a variety of plants.

Pythium debaryanum and *P. ultimum* are the species most often encountered. *P. debaryanum* is distinguished from *P. ultimum* by its plurality of

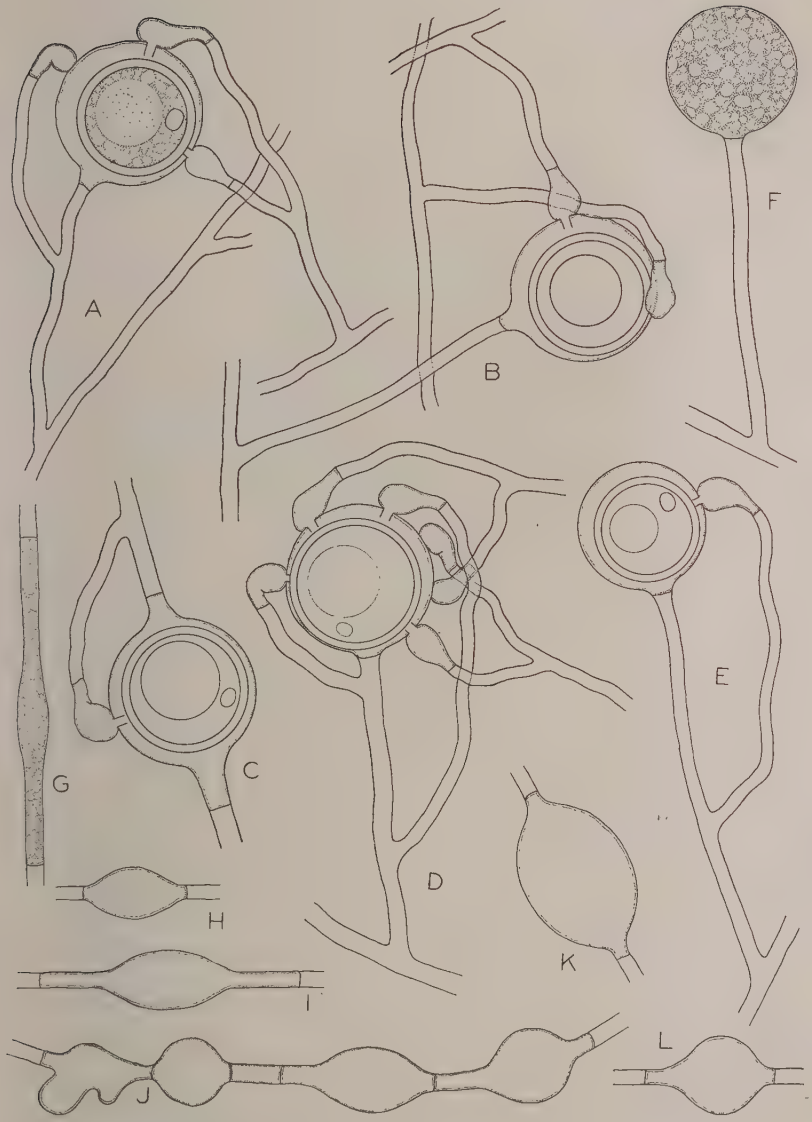

FIG. 12. *Pythium debaryanum*. *A–E*, Typical sexual stages. *F–L*, Sporangial types.

antheridia which are mono- or diclinous; when monoclinous they are stalked and originate some distance from the oogonium. *P. ultimum* usually has only a single antheridium which characteristically arises adjacent to the oogonium, is sessile and peculiarly shaped. Butler (1913) and Drechsler (1927) report similar observations on the antheridia of these two species. Van Luijk (1934b) believes the antheridial character insufficient for specific segregation, preferring to consider *P. ultimum* synonymous with *P. debaryanum*.

Pythium debaryanum may also be separated from *P. vexans* on the basis of antheridial differences. The antheridium of *P. debaryanum* has a narrow apex which is lightly applied to the oogonial wall, whereas the antheridium of *P. vexans* has a bell-shaped apex which is closely appressed and frequently fused with the oogonial wall. These two species differ in growth habits but not in temperature-growth relations.

Pythium araiosporon resembles *P. debaryanum* morphologically and in its growth habit and temperature values; it is considered synonymous with *P. debaryanum*.

Pythium fabae is indistinguishable morphologically from *P. debaryanum* and also resembles it in its habit of growth and responses to cardinal temperatures.

Pythium debaryanum var. *pelargonii* is reported by Braun (1925) to differ from *P. debaryanum* in the occurrence of sporangia with greater variation in size, in the position of the antheridial branch which adheres to the oogonium, and the presence of irregular swollen intercalary bodies. None of these points is sufficiently distinctive to segregate this variety from the species; additional evidence of their similarity is supplied by their temperature-growth relations. This variety is considered synonymous with *P. debaryanum*.

Although *Pythium marchantiae* and *P. cactacearum* are not well known species, the descriptions indicate that they are very similar to *P. debaryanum* and should be considered synonymous.

The writer follows Butler (1907) and Matthews (1931) in listing the other synonymous species.

The hosts from which *Pythium debaryanum* is known are presented below:

Acer sp. BULGARIA: Christoff (1933).
Agropyron caninum (L.) Beauv. UNITED STATES: Fischer *et al.* (1942).
A. ciliare (Trin.) Franch. UNITED STATES: Fischer *et al.* (1942).
A. cristatum (L.) Gaertn. UNITED STATES: Buchholtz (1942b); Fischer *et al.* (1942).
A. desertorum (Fisch.) Schult. UNITED STATES: Fischer *et al.* (1942).
A. inerme (Scribn. and Sm.) Rydb. UNITED STATES: Sprague.
A. intermedium (Host.) Beauv. UNITED STATES: Sprague.
A. michnoi Roshev. UNITED STATES: Sprague.
A. repens (L.) Beauv. UNITED STATES: Fischer *et al.* (1942).
A. riparium Scribn. and Sm. UNITED STATES: Fischer *et al.* (1942).
A. semicostatum (Steud.) Nees UNITED STATES: Sprague.
A. sibiricum (Willd.) Beauv. UNITED STATES: Fischer *et al.* (1942).
A. smithii Rydb. UNITED STATES: Fischer *et al.* (1942).

A. trachycaulum (Lk.) Malte UNITED STATES: Sprague.
A. trichophorum (Link) Richt. UNITED STATES: Fischer *et al.* (1942).
Agrostis alba L. UNITED STATES: Fischer *et al.* (1942).
A. stolonifera L. NETHERLANDS: van Luijk (1934a).
Amaranthus sp. GERMANY: de Bary (1881b).
A. caudatus L. UNITED STATES: Edson and Wood (1937).
Ananas comosus Merr. HAWAII: Carpenter (1919); Parris (1940); Sideris (1932).
Andropogon furcatus Muhl. UNITED STATES: Fischer *et al.* (1942).
A. halli Hack. UNITED STATES: Fischer *et al.* (1942).
A. scoparius Michx. UNITED STATES: Fischer *et al.* (1942).
Antirrhinum majus L. RHODESIA: Hopkins (1941). UNITED STATES: Sprague (1942a).
Apium graveolens L. var. *dulce* DC. UNITED STATES: Edson and Wood (1936); Foster and Weber (1924). SWEDEN: Hammarlund (1933).
Aquilegia vulgaris L. NETHERLANDS: Meurs (1928).
Arabis alpina L. NETHERLANDS: Meurs (1928).
Arrhenatherum elatius (L.) Mert. UNITED STATES: Fischer *et al.* (1942).
Aster sp. (?) UNITED STATES: Sprague (1942a).
Atropa belladonna L. UNITED STATES: Middleton (1941a).
Avena nuda L. UNITED STATES: Sprague.
A. sativa L. DENMARK: Gram and Rostrup (1922a, 1924). NETHERLANDS: Brandenburg (1931a). UNITED STATES: Melhus, Reddy and Buchholtz (1939); Melhus *et al.* (1940); Nance (1940); Sprague (1942a); Welch (1940, 1942); Author.
Begonia sp. GERMANY: Flachs (1931); Pape (1927b, 1933). UNITED STATES: Braun (1925).
B. semperflorens Link and Otto. UNITED STATES: Maneval (1940); Middleton, Tucker and Tompkins (1938, 1942); Swift (1932).
Berberis gracilis Hartw. UNITED STATES: Middleton (1938); Nance (1939).
Beta vulgaris L.: AUSTRIA: Fischer (1931); Miestinger *et al.* (1932). BELGIUM: Decoux, Vanderwaeren and Roland (1935, 1936, 1938); Marchal (1929). BULGARIA: Savoff (1924). CZECHOSLOVAKIA: Stehlik (1934); Stehlik and Neuwirth (1929, 1931). DENMARK: Anonymous (1926a); Gram (1926, 1927a, 1927b, 1928, 1937); Gram and Rostrup (1922b, 1923, 1924); Rostrup (1895–6). ENGLAND: Beaumont (1937); Beaumont and Hodson (1931); Petherbridge and Stirrup (1935); Staniland and Beaumont (1938); Woodward and Dillon-Weston (1929). GERMANY: Anonymous (1924b, 1926c, 1927a, 1927b, 1927c, 1930, 1932, 1936c); Appel (1929); Barkhoff (1928); Busse, Peters and Ulrich (1911); Esmarch (1925); Gehring and Brothuhn (1922, 1924); Greis (1939); Gropp (1929); Hecke (1923); Korff and Böning (1930); Kuster (1927); Laske (1936); Lhode (1874); Molz (1927, 1929); Neuwirth (1933); Oberdorfer (1930, 1931); Otto (1930); Peters (1906, 1911, 1924); Plaut (1929); Schaffnit and Meyer-Hermann (1930); Schille (1939); Schmidt (1934); Stocklasa (1898); Voelkel and Klemm (1932). IRELAND: Gallagher (1929), Greeves and Muskett (1936); Hughes (1935); Murphy (1927). ITALY: Campanile (1923). NETHERLANDS: de Haan (1935); Meijer (1934); Meurs (1928); Verhoeven (1927). SCOTLAND: Foister (1941). SWEDEN: Arrhenius (1923); Hammarlund (1933). SWITZERLAND: Gaümann (1928). UNITED STATES: Brandes and Coons (1934); Buchanan (1935, 1938); Buchholtz (1938); Campbell (1939); Clinton (1916); Coons (1924); Coons and Stewart (1927); Doran (1936); Edson (1913, 1915a, 1915b); Edson and Wood (1936); Hartwell and Damon (1914); Johnson (1914a); La Clerg (1937, 1939); Nance (1940); Rumbold (1924); Stewart (1931); Young (1940); Author.
Bouteloua curtipendula (Michx.) Torr. UNITED STATES: Fischer *et al.* (1942).
B. gracilis (H.B.K.) Lag. UNITED STATES: Fischer *et al.* (1942).
Brassica caulorapa Pasq. UNITED STATES: Johnson (1914a).
B. juncea (L.) Coss. PHILIPPINE ISLANDS: Ramos (1926).
B. napus L. GERMANY: Klemm (1938).
B. oleracea L. var. *botrytis* L. DENMARK: Jorgenson (1933). GERMANY: Kryopoulous (1916). RUSSIA: Bubentzoff (1935). UNITED STATES: Johnson (1914a); Author.
B. oleracea var. *capitata* L. DENMARK: Ferdinandsen (1923). GERMANY: Nicolaisen (1925). PHILIPPINE ISLANDS: Ramos (1926). PUERTO RICO: Cook (1939). SWEDEN: Hammarlund (1933). UNITED STATES: Drechsler (1926); Hoffman (1912); Johnson (1914a); Walker (1927); Author.

B. oleracea var. *gemmifera* Zenker. Canada: Godbout (1930).
B. pekinensis Rupr. Philippine Islands: Ramos (1926).
B. rapa L. Germany: Klemm (1938). Philippine Islands: Ramos (1926). United States: Johnson (1914a).
Bromus arvensis L. United States: Fischer *et al.* (1942).
B. carinatus Hesse. United States: Sprague.
B. erectus Huds. United States: Sprague.
B. inermis Leyss. United States: Fischer *et al.* (1942).
B. japonicus Thurb. United States: Sprague.
Cajanus cajan Millsp. Hawaii: Parris (1940); Sideris (1932).
Camelina sativa L. Germany: Frank (1881); Hesse (1874); Zopf (1890).
Canavalia ensiformis DC. Hawaii: Parris (1940); Sideris (1932).
Cannabis sativa L. Germany: Schultz (1939).
Capsella bursa-pastoris L. Germany: de Bary (1881b); Zopf (1890).
Capsicum annuum L. India: Narasimhan (1934). Italy: Petri (1935). Philippine Islands: Ramos (1926). United States: Edson and Wood (1936); Erwin (1932); Lehman (1921); Nance (1940); Author.
Carathamus tinctorius L. Philippine Islands: Ramos (1926).
Carica papaya L. Hawaii: Parris (1940); Sideris (1932). Philippine Islands: Ramos (1926); Reinking (1918).
Celosia cristata L. Philippine Islands: Ramos (1926).
Centaurea margaritacea Tenore. Italy: Voglino (1908).
Cereus sp. Italy: Flachs (1935).
C. grandiflorus. Italy: Preti (1932).
C. marginatus. Italy: Preti (1932).
C. spachianus. Italy: Preti (1932).
Chrysanthemum sp. Netherlands: Buisman (1927). United States: Sprague (1942a).
Cichorium endiva L. United States: Johnson (1914a).
Citrullus vulgaris Schrad. United States: Walker and Weber (1931).
Citrus sinensis Osbeck. Italy: Petri (1935).
Clarkia sp. India: Butler and Bisby (1931).
C. elegans Dougl. United States: Lewis (1937).
Coleus sp. United States: Braun (1925).
Colocasia esculenta Schott. Hawaii: Parris (1940). United States: Nance (1940).
Coriandrum sativum L. Philippine Islands: Ramos (1926).
Crotalaria anagyroides L. Philippine Islands: Ramos (1926).
C. toxicaria. Sumatra: Palm (1926).
Cucumis melo L. var. *reticulatus* Naud. Canada: Godbout (1930). United States: Edson and Wood (1936).
C. sativus L. Canada: Godbout (1930). England: Smith (1900). Czechoslovakia: Anonymous (1931). Norway: Schoyen (1897). United States: Allen and Haenseler (1935). Anonymous (1929); Braun (1925); Edson and Wood (1936); Garman (1901); Haenseler (1930); Humphrey (1892); Johnson (1914a); Author.
Cucurbita maxima Duchesne. United States: Johnson (1914a).
C. pepo L. United States: Johnson (1914a).
Dahlia sp. England: Ward (1883). Netherlands: van Poeteren (1935).
Daucus carota L. England: Ward (1883). United States: Author.
Dianthus caryophyllus L. Germany: Pape (1925). United States: Johnson (1914a).
Echinochloa crus-galli (L.) Beauv. United States: Fischer *et al.* (1942).
Elymus canadensis L. United States: Sprague.
E. dahuricus Turcz. United States: Sprague.
E. glaucus Buckl. United States: Sprague.
E. junceus Fisch. United States: Fischer *et al.* (1942).
E. macounii Vasey. United States: Fischer *et al.* (1942).
E. sibiricus L. United States: Sprague.
Equisetum sp. Germany: Frank (1881).
E. arvense. England: Smith (1876). Germany: Sadebeck (1874, 1875).
E. limosum. Germany: Sadebeck (1876, 1881).

E. palustre. GERMANY: Sadebeck (1874, 1875, 1876, 1881).
Eschscholzia californica Cham. NETHERLANDS: Meurs (1928).
Euphorbia pulcherrima Willd. UNITED STATES: Author.
Fern. UNITED STATES: Matthews (1931).
Festuca duriuscula L. NETHERLANDS: van Luijk (1934a).
F. elatior L. UNITED STATES: Fischer *et al.* (1942).
F. elatior var. *arundinacea* (Schren.) Wimm. UNITED STATES: Fischer *et al.* (1942).
F. octoflora Walt. UNITED STATES: Sprague.
F. rubra L. var. *commutata* Gaud. UNITED STATES: Fischer *et al.* (1942).
Fragaria chiloensis Duchesne. SCOTLAND: Wardlaw (1928).
Geranium sp. NETHERLANDS: Buisman (1927).
Gilia sp. INDIA: Butler and Bisby (1931). UNITED STATES: Atkinson (1895); Galloway (1891).
Gloxinia sp. NETHERLANDS: Meurs (1928).
Godetia willdenowiana Spach. NETHERLANDS: Meurs (1928).
Gossypium sp. BARBADOS: Lewton (1903). ANGLO-EGYPTIAN SUDAN (?): Andrews and Clouston (1938).
Gypsophila alba. UNITED STATES: Edson and Wood (1936).
Haplomitrium hookeri Nees. POLAND: Lilienfield (1911).
Hedera helix L. UNITED STATES: Maneval (1937).
Hibiscus esculentus L. PHILIPPINE ISLANDS: Ramos (1926).
Hordeum bulbosum L. UNITED STATES: Fischer *et al.* (1942).
H. distichon L. UNITED STATES: Sprague.
H. jubatum L. UNITED STATES: Sprague.
H. vulgare L. DENMARK: Gram and Rostrup (1922a, 1924).
Impatiens balsamina L. UNITED STATES: Johnson (1914a).
I. sultani Hook. ENGLAND: Pim (1888).
Insect cadavers. DENMARK: Petersen (1910).
Ipomoea batatas Lam. HAWAII: Parris (1940); Sideris (1932). UNITED STATES: Harter (1924); Author.
Iris pseudacorus L. SWEDEN: Palm (1935).
Koeleria cristata (L.) Pers. UNITED STATES: Sprague.
Lactuca sativa L. ENGLAND: Abdel-Salam (1933). PHILIPPINE ISLANDS: Ramos (1926). UNITED STATES: Byars and Gilbert (1920); Johnson (1914a); Matthews (1931); Weber and Foster (1928).
Lens esculenta Mnsh. NETHERLANDS: Meurs (1928).
Lepidium sativum L. GERMANY: de Bary (1881b); Lhode (1874); Zopf (1890). INDIA: Butler (1907, 1913); Butler and Bisby (1931). IRELAND: Muskett, Carrothers and Cairns (1932). UNITED STATES: Doran (1936); Hemmi (1923); Johnson (1914a).
Lilium longiflorum Thunb. UNITED STATES: Author.
L. regale Wils. UNITED STATES: van Hook (1930).
Linum usitatissimum L. CANADA: Bisby *et al.* (1938); Vanterpool (1935b). NETHERLANDS: Diddens (1932). RUSSIA: Kletschetow (1924). UNITED STATES: Buchanan (1938); Edson and Wood (1936, 1937); Wood and Nance (1938).
Lobelia sp. UNITED STATES: Atkinson (1895); Galloway (1891).
Luffa acutangula Roxb. PHILIPPINE ISLANDS: Ramos (1926).
Lupinus sp. GERMANY: Pape (1927a). UNITED STATES: Gould (1940); Middleton (1938); Nance (1939).
L. angustifolius. GERMANY: Noll (1939); Schultz (1939).
L. luteus L. GERMANY: Schultz (1939).
L. polyphyllus Lindl. NETHERLANDS: Meurs (1928).
L. texensis Hook. UNITED STATES: Taubenhaus and Ezekiel (1932).
Lycopersicon esculentum Mill. CANADA: Berkeley (1925). DENMARK: Weber (1922, 1924). PHILIPPINE ISLANDS: Reinking (1919); Ramos (1926). PUERTO RICO: Cook (1939). SWEDEN: Hammarlund (1933). UNITED STATES: Byars and Gilbert (1920). Horne, Essig, and Herms (1923); Johnson (1914a); Middleton (1938); Mumford (1934, 1935); Nance (1939); Weber and Ramsey (1926).
Marchantia polymorpha L. FRANCE: Nicolas (1926, 1927).

Medicago sativa L. MAURITIUS: Anonymous (1925a). NETHERLANDS: van Luijk (1938a, 1938b). UNITED STATES: Buchholtz (1942a); Buchholtz and Meredith (1938); Maneval (1937); Melhus, Reddy and Buchholtz (1939); Middleton (1938); Nance (1939).

Musa cavendishii Lamb. HAWAII: Carpenter (1919).

Nicotiana rustica L. RUSSIA: Kuprianoff and Gorelnko (1930); Grushevoy (1938).

N. tabacum L. CANADA: Anonymous (1927d); Nelson, Major and McRae (1931). GERMANY: Böning (1928, 1931, 1935); Kotte (1929). INDIA: Hector (1931). ITALY: Trotter (1938). MAURITIUS: Corbett (1937). PHILIPPINE ISLANDS: Clara (1925); David and Roldan (1926); Ramos (1926); Reinking (1919). PUERTO RICO: Cook (1931, 1939); Edson and Wood (1937); Gage (1939); Nolla (1932). RHODESIA: Hopkins (1927, 1930). ROUMANIA: Banu and Constantinescu (1935); Ghimpu (1939); Knechtel (1914); Savulescu (1930). RUSSIA: Grushevoy (1938); Kuprianoff and Gorelnko (1930); Zaprometoff (1926). SUMATRA: Jochems (1926, 1927a, b); Van der Goot (1928); Van Hall (1925). TURKEY: Perrin and Osman (1928). UNION SOUTH AFRICA: Moore and Smith (1933). UNITED STATES: Anderson and Clinton (1926); Anderson, Swanback and Street (1929); Clinton and Anderson (1927); Edson and Wood (1936, 1937); Johnson (1914a, b, 1924); Sideris (1932).

Opuntia sp. UNITED STATES: Author.

Oryza sativa L. HAWAII: Carpenter (1919). PHILIPPINE ISLANDS: Ramos (1926).

Oryzopsis hymenoides (Roem. and Schult.) Rick. UNITED STATES: Fischer *et al.* (1942).

O. miliacea (L.) Benth. and Hook. UNITED STATES: Fischer *et al.* (1942).

Pachyrrhizus angulatus Rich. PHILIPPINE ISLANDS: Ramos (1926).

Panicum capillare L. UNITED STATES: Fischer *et al.* (1942).

P. miliaceum L. GERMANY: Frank (1881); Hesse (1874); Zopf (1890). UNITED STATES: Sprague (1942a).

P. virgatum L. UNITED STATES: Fischer *et al.* (1942).

Pelargonium sp. ENGLAND: Buddin and Wakefield (1924); Ward (1883). GERMANY: Pape (1931); Peters (1910). NETHERLANDS: van Poeteren (1922). UNITED STATES: Braun (1925); Johnson (1914a).

P. domesticum Bailey: UNITED STATES: Gill (1936).

P. graveolens L'Hér. UNITED STATES: Gill (1936).

P. hortorum Bailey. UNITED STATES: Gill (1936).

P. zonale L'Hér. CANADA: Bisby *et al.* (1938).

Phalaris arundinacea L. UNITED STATES: Fischer *et al.* (1942).

Phaseolus vulgaris L. NETHERLANDS: Meurs (1928). PHILIPPINE ISLANDS: Ramos (1926). PUERTO RICO: Cook (1939). SWEDEN: Hammarlund (1933). UNION SOUTH AFRICA: Wager (1940). UNITED STATES: Harter and Whitney (1927a); Johnson (1914a); Moore (1938); Author.

Phragmites communis Trin. UNITED STATES: Sprague.

Phyllocactus phyllanthoides Link. ITALY: Preti (1936).

Picea sp. BULGARIA: Christoff (1933). UNITED STATES: Anonymous (1928); Edson and Wood (1936, 1937).

P. canadensis Link. UNITED STATES: Hoffman (1912). Toumey and Li (1924).

P. engelmanni Engelm. UNITED STATES: Gravatt (1925); Hartley (1921); Hartley and Pierce (1917); Rathbun (1923); Rathbun-Gravatt (1925); Spaulding (1914).

P. excelsa Link. SWITZERLAND: Roth (1935a, 1935b).

P. parryana (Andre) Parry. UNITED STATES: Hartley (1921); Hartley and Pierce (1917); Spaulding (1914).

P. sitchensis (Bong.) Carr. UNITED STATES: Hartley (1921); Hartley and Pierce (1917); Spaulding (1914).

Pinus sp. BULGARIA: Dimitroff and Bioltscheff (1936). UNITED STATES: Pierce and Hartley (1919); Hartley and Merrill (1914); Anonymous (1928); Hartley (1912a).

P. banksiana Ait. UNITED STATES: Fischer, P. L. (1941); Gravatt (1925); Hartley, Merrill and Rhoads (1918); Rathbun (1922, 1923); Rathbun-Gravatt (1925).

P. insularis Endl. PHILIPPINE ISLANDS: Roldan (1933).

P. massoniana Lamb. PHILIPPINE ISLANDS: Roldan (1933).

P. nigra Arn. var. *austriaca*. ITALY: Sibilia (1928). UNITED STATES: Wilde and White (1939).

P. ponderosa Dougl. UNITED STATES: Fischer, P. L. (1941); Hartley, Merrill and Rhoads (1918); Hoffman (1912).
P. resinosa Ait. UNITED STATES: Eliason (1928); Fischer P. L. (1941); Gravatt (1925); May and Young (1927); Rathbun (1922, 1923); Rathbun-Gravatt (1925); Tilford (1938); Wilde and White (1939).
P. strobus L. BULGARIA: Christoff (1933). UNITED STATES: Toumey and Li (1924); Wilde and White (1939).
P. sylvestris L. BULGARIA: Christoff (1933). NETHERLANDS: Ten Houten (1939).
Pisum arvense L. SWEDEN: Hammarlund (1933).
P. sativum L. CANADA: Stone (1924). ENGLAND: Baylis (1941); Carruthers (1899). GERMANY: Noll (1939). NETHERLANDS: Meurs (1928). SWEDEN: Hammarlund (1933). UNITED STATES: Anonymous (1923); Drechsler (1925); Harter and Whitney (1927a); Matthews (1931); Sturgis (1898); Vaughn (1924).
Poa ampla Merr. UNITED STATES: Fischer *et al.* (1942).
P. bulbosa L. UNITED STATES: Fischer *et al.* (1942).
P. palustris L. UNITED STATES: Fischer *et al.* (1942).
P. pratensis L. UNITED STATES: Sprague.
P. secunda Presl. UNITED STATES: Fischer *et al.* (1942).
Polianthes tuberosa L. UNITED STATES: Edson and Wood (1936).
Pseudotsuga taxifolia Britt. UNITED STATES: Eliason (1928); Hartley (1921); Hartley and Pierce (1917); Pierce and Hartley (1919); Spaulding (1914).
Psophocarpus tetragonolobus DC. PHILIPPINE ISLANDS: Ramos (1926).
Pyrus communis L. BELGIUM: Marchal and Marchal (1921).
Ranunculus asiaticus L. UNITED STATES: Tompkins and Middleton (1939, 1942).
Raphanus sativus L. PHILIPPINE ISLANDS: Ramos (1926). SWEDEN: Hammarlund (1933). UNITED STATES: Braun (1925); Hoffman (1912).
Ricinus communis L. INDIA: Butler (1913).
Robinia sp. GERMANY: Hiltner (1902).
Saccharum officinarum L. HAWAII: Carpenter (1919, 1921); Parris (1940); Sideris (1932). UNITED STATES: Rands (1930); Rands and Dopp (1938b); Stevenson and Rands (1938).
Salsola tragus L. UNITED STATES: Hoffman (1912).
Salvia sclarea L. ITALY: Voglino (1923).
Satureia hortensis L. ITALY: Voglino (1923).
Schedonnardus paniculatus (Nutt.) Trel. UNITED STATES: Sprague.
Secale cereale L. UNITED STATES: Sprague.
S. montanum Guss. UNITED STATES: Sprague.
Selaginella sp. NETHERLANDS: van Poeteren (1923).
Setaria italica (L.) Beauv. UNITED STATES: Fischer *et al.* (1942).
S. viridis (L.) Beauv. UNITED STATES: Fischer *et al.* (1942).
Sinapis sp. GERMANY: Lhode (1874).
Soil. GERMANY: Butler (1907). UNITED STATES: Harvey (1925, 1927, 1929); Matthews (1931); Meredith (1938, 1940); Raper (1928); Author.
Solanum melongena L. PHILIPPINE ISLANDS: Ramos (1926). PUERTO RICO: Cook (1939); UNITED STATES: Drechsler (1926).
S. tuberosum L. AUSTRALIA: Bald (1941); Fish, Pugsley and Tyland (1937). CANADA: Dickson (1922); Sanford (1924). ENGLAND: Chona (1932); Pethybridge and Smith (1930); Ward (1883). GERMANY: de Bary (1881); Sadebeck (1875); Zopf (1890). HAWAII: Parris (1940); Sideris (1932). SWEDEN: Hammarlund (1933). TASMANIA: Bald (1941); Dowson (1931). UNITED STATES: Anonymous (1925b); Hawkins (1916, 1917); Hawkins and Harvey (1919); Orton (1909); Porter and Schneider (1939); Schade (1936); Shapovalov and Link. (1924).
Sorghum vulgare L. MANCHURIA: Miuri (1921). UNITED STATES: Fischer *et al.* (1942).
S. vulgare var. *sudanense* (Piper) Hitchc. UNITED STATES: Fischer *et al.* (1942).
Soya max L. UNITED STATES: Lehman and Wolfe (1926); Morse and Cartter (1939); Sprague (1942b); Wolf and Lehman (1924).
Sparganium simplex Huds. SWEDEN: Palm (1935).
Spergula arvensis L. GERMANY: Frank (1881); Hesse (1874); Zopf (1890).

Spinacea oleracea L. CANADA: Godbout (1930). NETHERLANDS: Meurs (1928). UNITED STATES: Author.
Stanhopea saccata Batem. GERMANY: Lhode (1874).
Stapelia sp. UNION SOUTH AFRICA: Wager (1940).
Stipa viridula Trin. UNITED STATES: Fischer *et al.* (1942).
Tecoma stans L. PHILIPPINE ISLANDS: Ramos (1926).
Tilia europaea L. UNITED STATES: Spaulding (1914).
T. ulmifolia Scop. UNITED STATES: Spaulding (1914).
Trifolium hybridum L. GERMANY: Zopf (1890).
T. pratense L. UNITED STATES: Melhus, Reddy and Buchholtz (1939).
T. repens L. GERMANY: Frank (1881); Hesse (1874); Zopf (1890).
Trigonella foenum-graceum L. UNITED STATES: Hartley (1921).
Tsuga canadensis Carr. UNITED STATES: Toumey and Li (1924); Hartley (1921).
T. mertensiana (Bong.) Sarg. UNITED STATES: Hartley and Pierce (1917); Pierce and Hartley (1919); Spaulding (1914).
Tulipa gesneriana L. (?). ENGLAND: Moore and Buddin (1937).
Vicia faba L. AUSTRALIA: Cheney (1932). GERMANY: Noll (1939). HAWAII: Parris (1940); Sideris (1932). UNITED STATES: Author.
Vigna sp. UNITED STATES: Hartley (1921).
V. sinensis Endl. HAWAII: Parris (1940); Sideris (1932). PHILIPPINE ISLANDS: Ramos (1926). UNITED STATES: Author.
Viola cornuta L. NETHERLANDS: Meurs (1928).
V. tricolor. GERMANY: Kaven (1934); Flachs (1931). NETHERLANDS: van Eek (1938). NORWAY: Solberg (1927). UNITED STATES: Author.
Viscaria sp. UNITED STATES: Atkinson (1895); Galloway (1891).
Vitis vinifera L. GREECE: Sarejanni (1936).
Zea mays L. GERMANY: Frank (1881); Hesse (1874); Zopf (1890). HAWAII: Parris (1940); Sideris (1932). ITALY: Curzi (1929). MANCHURIA: Miuri (1921). PHILIPPINE ISLANDS: Ramos (1926). RUSSIA: Speschneff (1896–97). UNITED STATES: Buchanan (1938); Ho (1941); Ho and Melhus (1940); Melhus (1940); Sprague; Author.

Pythium debaryanum is reported from seedlings in Canada (Bisby *et al.*, 1938) in Denmark (Jørstad, 1922), in Scotland (Anonymous, 1926b), in the United States (Marsh, 1937; Raeder, 1921), and in Puerto Rico and the Virgin Islands (Seaver *et al.*, 1932). *P. debaryanum* is reported from conifers in Denmark (Jørstad, 1925), and in the United States (Hartley 1910, 1912b; Hartley and Hahn, 1919) and from broad leaf tree seeds in Russia (Sokoloff, 1940).

47. PYTHIUM CYSTOSIPHON (Roze and Cornu) Lindstedt, Synopsis der Saprolegniaceen und Beobactungen uber einige Arten. 1872.

Cystosiphon pythioides Roze and Cornu, Ann. Sci. Nat. V. **11**: 72–91. 1869.
Pythium pythioides Ramsbottom, Trans. Brit. Mycol. Soc. **5**: 304. 1916.

Hyphae endophytic, rarely septate, perforating the cells of the host. Sporangia usually spherical, never prolate ellipsoidal, formed in the peripheral host cells, producing a single tube which bears the exogenous vesicle; zoospores 1 to 49, elongate, 8 to 16 μ long, more or less reniform, biciliate. Oogonia spherical, terminal or intercalary. Antheridia diclinous, 1 to 3 per oogonium, borne terminally on branches of varying length. Oospores aplerotic, single, provided with a thick, reticulately sculptured wall.

Parasitic in *Lemna arrhiza* L., *L. gibba* L., *L. minor* L., and *Riccia fluitans* L., France.

Roze and Cornu created *Cystosiphon* as a new genus intermediate between the Saprolegniaceae and Peronosporaceae. Lindstedt pointed out the synonymity of the genera *Cystosiphon* and *Pythium* transferring *C. pythiodes* to *P. cystosiphon.*

The species is unique among spheroidal sporangial forms in possessing an oospore with a reticulate wall.

Pythium cystosiphon apparently has not been reported since the original description.

48. PYTHIUM ACANTHICUM Drechsler, Jour. Wash. Acad. Sci. 20: 398–418. 1930.

Hyphae measuring 1.3 to 5.6 μ in diameter. Sporangia typically intercalary though sometimes acrogenous, then subspherical measuring 12 to 43 μ in diameter, when intercalary usually composed of a subspherical part and a contiguous portion of the hypha, short or up to 75 μ long, sometimes composed of 2 or more subspherical portions associated by means of a communicating hypha; zoospores 5 to 50, biciliate, reniform and longitudinally grooved, measuring 8 to 9.5 μ in diameter upon encystment. Oogonia acrogenous but typically intercalary or laterally or tangentially intercalary, subspherical with an echinulate wall, measuring 13 to 30 μ, average 23.7 μ, in diameter excluding the spines which are 1.5 to 5 μ, average 2.7 μ, in length and average 1.9 μ in basal diameter, tapering slightly to a rounded apex. Antheridia typically monoclinous, occasionally diclinous, 1 to 2, usually 1 per oogonium, borne terminally on branches 6 to 25 μ, usually 10 to 15 μ, long, the antheridial cell inflated clavate, straight or crook-necked, 8 to 17 μ long and 5 to 9 μ wide, the larger cells frequently lobate due to 1 or 2 transverse constrictions, the apex broadly applied, sometimes the entire cell longitudinally applied to the oogonium. Oospores plerotic though usually free from the oogonial wall, single, measuring 12 to 27 μ, average 21.7 μ, in diameter, provided with a moderately thickened wall, measuring 1.3 to 2 μ, average 1.6 μ, thick and containing a single reserve globule and refringent body; germination by means of germ tubes or zoospores.

Originally described from fruits of *Citrullus vulgaris* Schrad., United States.

A number of isolates of this species were available for study. The sporangia of *Pythium acanthicum* are very distinctive and readily separate the species from all other echinulate oogonial forms with plerotic oospores. Similar sporangia are found in *P. oligandrum*, a species possessing echinulate oogonia and aplerotic oospores. This type of sporangium is termed contiguous because of the intimate association of the subspherical part with an attached hyphal element.

The oogonial protuberances of *Pythium acanthicum* are peculiar to the species, though those of *P. mamillatum* resemble them but differ in being longer and usually curved. The spines of *P. spinosum* differ strikingly from those of both the other species in their length and digitate character.

The antheridia of *Pythium acanthicum* are typically monoclinous, the antheridial stalk frequently bearing a branched, vegetative prolongation of

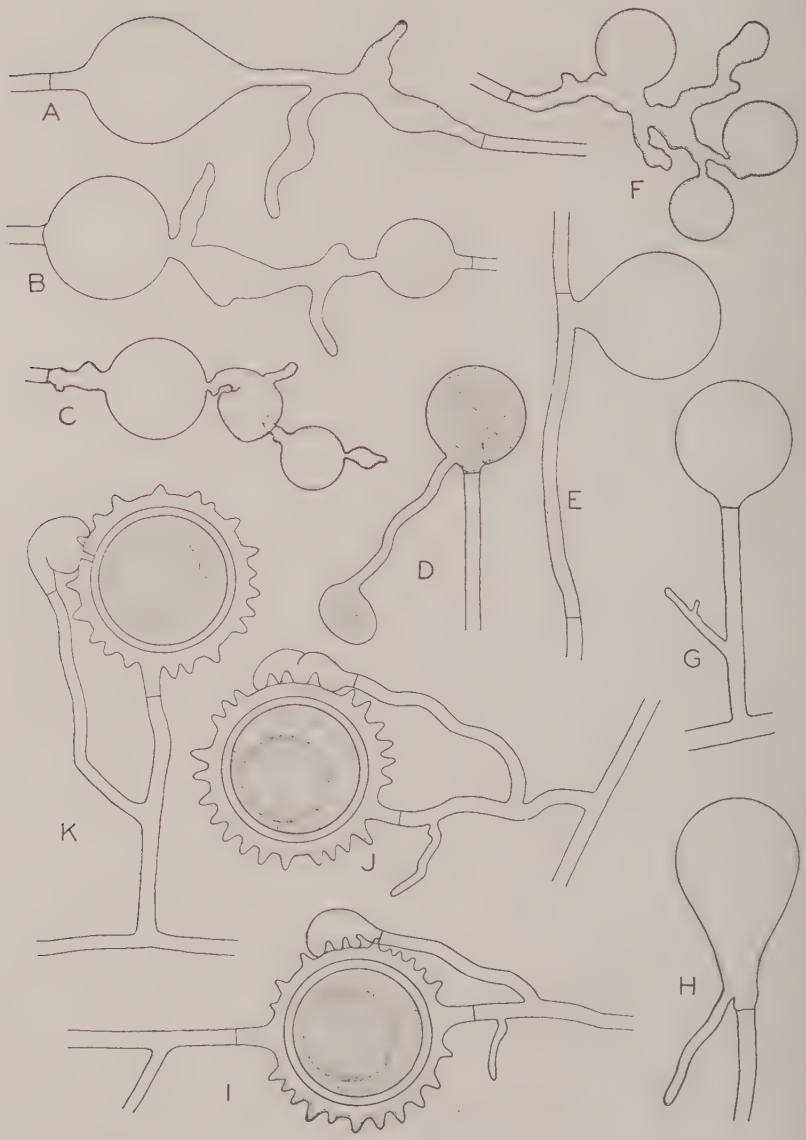

FIG. 13. *Pythium acanthicum*. *A–H*, Sporangia of typical morphology. *A*, *B*, *C*, *F*, Exemplify the typical contiguous sporangial habit. *I–K*, Oogonia, antheridia, and mature oospores.

varying length. No vegetative prolongations occur on the monoclinous antheridia of *P. mamillatum* and *P. spinosum*. The antheridial cell of *P. acanthicum* is inflated and frequently lobate with one or several transverse constrictions, differing decidedly from the less inflated, clavate, smooth, crook-necked antheridia of *P. mamillatum* and *P. spinosum*.

The mode of oospore germination in this species is twofold, by germ tubes and zoospores; the production of zoospore is the more common. Zoospore formation is usually accomplished in the same manner as displayed when originating from sporangia. Occasionally a saccate or irregularly defined bladder-like structure is produced in place of the normally spherical vesicle. Still other instances have been observed in which the germ tube gives rise to a spherical or saccate structure which in turn gives rise to an evacuation tube capped by a vesicle in which the zoospores are delineated; these observations are corroborated by the recent report and illustrations of Wager (1940).

The cumulous mycelial growth habit and the temperature-growth relations of *Pythium acanthicum* are useful adjuncts for the identification of this species.

Pythium acanthicum is known from *Citrullus vulgaris* Schrad. from the original report and a subsequent one by Drechsler (1939), and by the author in the United States, from *Dahlia* sp. and *Pisum sativum* L., by Wager (1940) in South Africa and by the author from *Phaseolus vulgaris* L. and *Solanum melongena* L. in the United States.

49. Pythium mamillatum Meurs, Wortelrot, Veroorzaakt door Schimmels uit de Geslachten *Pythium* Pringsheim en *Aphanomyces* de Bary. 1928.

Hyphae measuring 4 to 9.3 μ in diameter. Sporangia spherical, 14.3 to 20.7 μ, average 16.3 μ, in diameter, acrogenous, or intercalary; zoospores 5 to 14, reniform and laterally biciliate. Oogonia spherical, typically acrogenous and rarely intercalary, with an echinulate wall, the spines are conical and obtusely tipped, measuring 2.7 to 6.0 μ, average 4.4 μ, long, the oogonia measuring 13 to 19.3 μ, average 16.4 μ, in diameter, excluding the protuberances. Antheridia monoclinous, usually single and arising in close proximity to the oogonium, the stalk short, the cell clavate with the apex moderately applied to the oogonial wall. Oospores plerotic, single, with a moderately thick wall; germination not observed.

Originally described as causing damping-off of *Beta vulgaris* L. seedlings, Netherlands.

The sporangia of *Pythium mamillatum* are quite similar to those of *P. spinosum*, spherical to subspherical, acrogenous and intercalary. Zoospores are freely produced in *P. mamillatum* and rarely in *P. spinosum*, the sporangia of the latter germinating by means of 1 to 3 germ tubes. The presence of contiguous sporangia serves in distinguishing *P. acanthicum* from *P. mamillatum*.

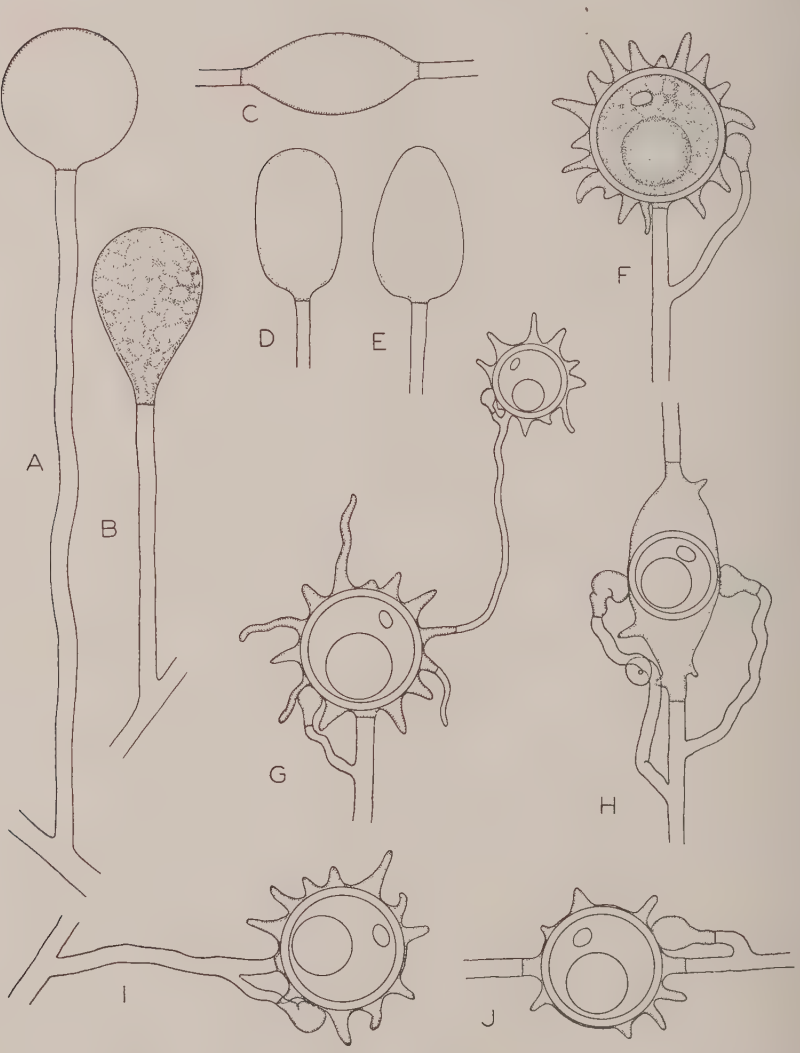

FIG. 14. *Pythium mamillatum*. *A–E*, Sporangia of usual occurrence. *A*, *B*, *C*, Most typical of the sporangial habits. *F–J*, The sexual apparatus. *F*, *I*, *J*, Demonstrate the typical monoclinous type of antheridia and the common types of oogonial echinulation. *H*, Infrequently produced intercalary oogonium with few spines, usually produced in aquatic substrate. *G*, Oogonium demonstrating the occasional proliferation of spines which may bear an oogonium which frequently contains an oospore.

The spherical, echinulate oogonia of *Pythium mamillatum* and *P. spinosum* are more often acrogenous than intercalary. The oogonial protuberances, however, are very different; they are conical, obtuse and about 4.4 μ long in *P. mamillatum*, while in *P. spinosum* they are digitate, obtuse and about 7 μ long. Occasionally the writer has observed spines of *P. mamillatum* to continue growth and give rise to a short filament which would infrequently give rise to an oogonium; mature oospores have been observed in such oogonia.

The antheridia of *Pythium mamillatum* are monoclinous, originating in close proximity to the oogonium; the antheridial stalk is short and upcurved, bearing an inflated, smooth, clavate, crook-necked antheridial cell which is narrowly applied to the oogonium. The antheridia of *P. spinosum* are more or less analogous, while those of *P. acanthicum* are decidedly different. The antheridia of *P. spinosum* are both monoclinous and diclinous, and do not originate as close to the oogonium as in *P. mamillatum;* the antheridial cell of *P. spinosum* is allantoid-clavate, slightly curved and narrowly applied to the oogonium.

Pythium mamillatum and *P. spinosum* may be distinguished also by their differences in growth habit and temperature-growth relationship.

This fungus has been observed on the following listed plants:

Ageratum houstonianum Mill. United States: Author.
Agrostis stolonifera L. Netherlands: van Luijk (1934a, 1938a).
Ananas comosus Merr. Hawaii: Parris (1940); Sideris (1932).
Antirrhinum majus L. United States: Author.
Aquilegia caerulea James. United States: Author.
Avena sativa L. Netherlands: Brandenburg (1931a).
Beta vulgaris L. Netherlands: Meurs (1928, 1929); van Poeteren (1930).
Cladophora sp. Sweden: Palm (1932).
Collinsia bicolor Benth. United States: Author.
Festuca duriuscula L. Netherlands: van Luijk (1934a).
Geum chiloense Balb. United States: Author.
Gleocapsa sp. Sweden: Palm (1932).
Linum usitatissimum L. Netherlands: Diddens (1932).
Medicago sativa L. United States: Author.
Pelargonium domesticum Bailey. United States: Gill (1936).
P. graveolens L'Hér. United States: Gill (1936).
P. hortorum Bailey. United States: Gill (1936).
Saccharum officinarum L. United States: Rands and Dopp (1938b); Stevenson and Rands (1938).
Soil. United States: Matthews (1931).
Triticum aestivum L. United States: Author.
Viola tricolor L. England: Chesters. United States: Author.

50. Pythium spinosum Sawada, Jour. Nat. Hist. Soc. Formosa **16**: 199–212. 1926.

Hyphae measuring 2.5 to 5.0 μ in diameter. Sporangia are spherical to subspherical when acrogenous, spherical to spindle-shaped when intercalary, measuring 14 to 33 μ, average 22.4 μ, in diameter, wall usually smooth but occasionally may bear digitate or blunt conical spines; zoospores rarely formed, germination usually accomplished by means of germ tubes. Oogonia

spherical to subspherical when acrogenous, sometimes limoniform when intercalary, measuring 13.2 to 27.4 μ, average 18.2 μ, in diameter, excluding the spines which are conical with obtuse apices or more commonly digitate, 5 to 8 μ long and 1.5 to 2 μ broad at the base. Antheridia terminal, typically monoclinous though sometimes diclinous, 1, rarely 2, per oogonium, originating close to the oogonium and measuring 12 to 32 μ long and 3 to 5 μ wide. Oospores plerotic, single, smooth-walled, measuring 10.1 to 25.3 μ, average 16.7 μ, in diameter; germination not observed.

Parasitic on seedlings of *Antirrhinum majus* L., Formosa.

The description given above is taken in large part from a translation of the original Japanese obtained through the courtesy of Dr. V. A. Wager. Supplementary information obtained from the writer's observations is also included. In the original description the oogonia are said to be 17 to 24 μ, average 19.7 μ, in diameter, including the spines which are 5 to 8 μ long; just how a plerotic oospore measuring 12 to 21 μ, average 16.6 μ, in diameter would be oriented in such an oogonium allowing for a minimum spine length and thickness of oogonial wall is not quite clear. The measurements given in the description presented above are taken from the author's study of the species.

Supplementary literature describing the species and giving its host range are found in an anonymous abstract in the Japanese Journal of Botany, **3**: 108–109, 1927, and Sawada (1927, 1931).

Pythium spinosum is distinguished from other echinulate oogonial forms with plerotic oospores by the characteristic long, digitate, obtuse oogonial protuberances.

The antheridium of *Pythium spinosum* differs from those of its congeners, *P. acanthicum* and *P. mamillatum*, in being rather long, narrow, allantoid, the apical portion not inflated or lobate. The antheridial stalk is devoid of the vegetative prolongations commonly observed in *P. acanthicum* and is longer and straighter than in *P. mamillatum*. Cook and Collins (1937) report that the antheridium of *P. spinosum* is stalked, androgynous (monoclinous) and rarely arises from the oogonial stalk. Apparently these authors have interpreted erroneously the meaning of androgynous (monoclinous) antheridia, for these are customarily defined as arising from the oogonial stalk.

The growth habit and temperature-growth relations of *Pythium spinosum* may be used to distinguish it from related species.

This species has been observed on the following plants:

Allium cepa L. United States: Author.
A. fistulosum L. Formosa: Sawada (1931); Sawada and Chen (1926).
A. schaenoprasum L. Formosa: Sawada (1931); Sawada and Chen (1926); Darker (1940).
Antirrhinum majus L. Formosa: Sawada (1931); Sawada and Chen (1926).
Arctium lappa L. Formosa: Sawada (1931).
Brassica campestris L. Formosa: Sawada (1931); Sawada and Chen (1926).
B. oleracea L. var. *capitata* L. Japan: Tasugi and Siino (1940).
Calendula officinalis L. Formosa: Sawada (1931). Japan: Tasugi and Siino (1940).
Callistephus chinensis Nees. Japan: Tasugi and Siino (1940).
Campanula medium L. Formosa: Sawada (1931).

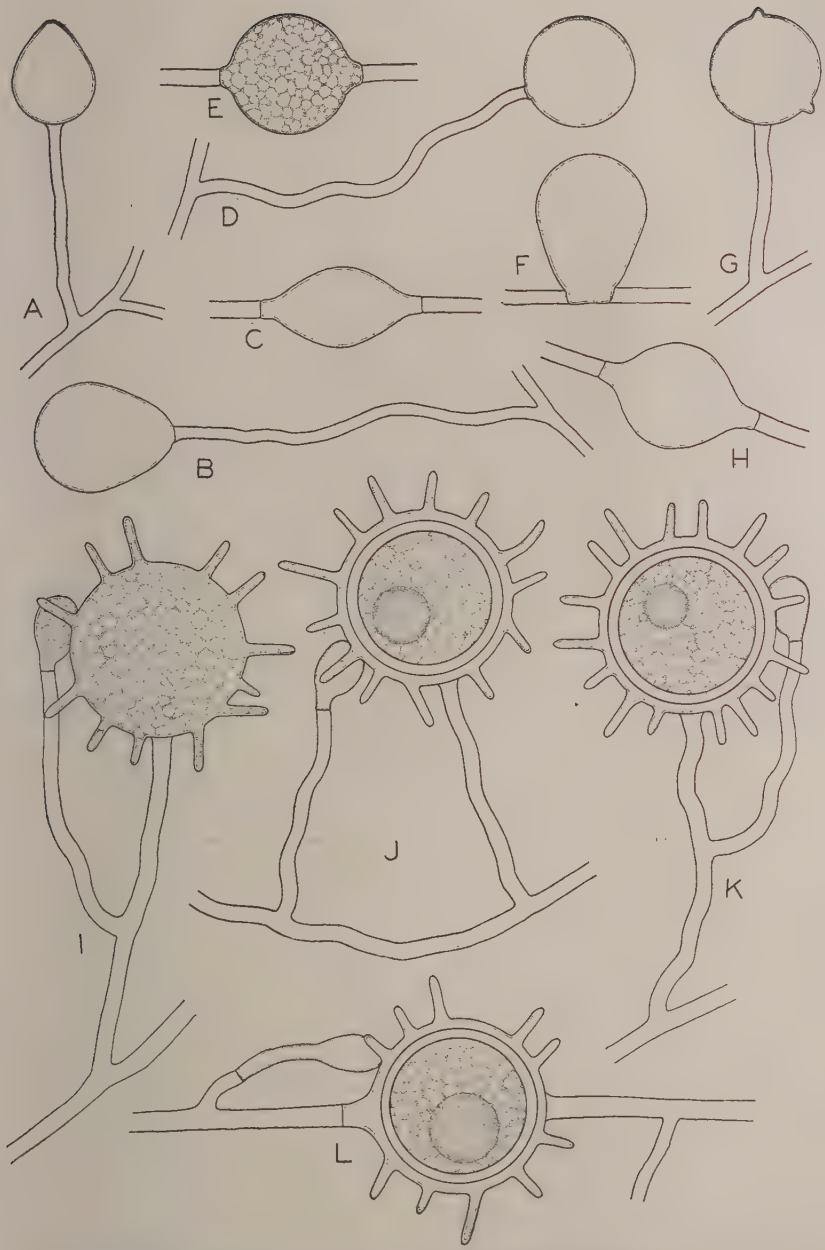

FIG. 15. *Pythium spinosum*. *A–H*, Sporangia showing typical morphology. *I–L*, Various stages in the development of the oospores. *I*, Immature oogonium with typical monoclinous antheridium. *J*, Antheridia of this type are of infrequent occurrence. *L*, Typical occasional intercalary sexual apparatus.

Carica papaya L. Union South Africa: Wager (1931, 1932a, 1940).
Chrysanthemum coronarium L. Formosa: Sawada (1931); Sawada and Chen (1926).
Citrullus vulgaris Schrad. United States: Author.
Coriandrum sativum L. Formosa: Sawada (1931).
Cucumis sativus L. Formosa: Sawada (1931); Sawada and Chen (1926). Japan: Tasugi and Siino (1940).
Daucus carota L. Formosa: Sawada (1931); Sawada and Chen (1926).
Dianthus chinensis L. Formosa: Sawada (1931); Sawada and Chen (1926).
Lactuca sativa L. Formosa: Sawada (1931); Sawada and Chen (1926). Japan: Tasugi and Siino (1940).
Lycopersicon esculentum Mill. Formosa: Sawada (1931). Japan: Tasugi and Siino (1940).
Papaver rhoeas L. Japan: Tasugi and Siino (1940).
Primula sinensis Lindl. England: Cook and Collins (1937).
Raphanus sativus L. Formosa: Sawada (1931); Sawada and Chen (1926).
Soil. Bohemia: Cejp (1931).
Solanum melongena L. Formosa: Sawada and Chen (1926). Japan: Tasugi and Siino (1940).
Zinnia elegans Jacq. Formosa: Sawada (1931). Japan: Tasugi and Siino (1940).

51. Pythium oligandrum Drechsler, Jour. Wash. Acad. Sci. **20**: 398–418. 1930.

Hyphae measuring 1.5 to 6.8 μ in diameter. Sporangia acrogenous, typically intercalary, subspherical, measuring 25 to 45 μ in diameter, usually consisting of 1 to 5 subspherical bodies together with a contiguous portion of a filament of varying length, 5 to 75 μ long, sometimes the filament irregularly swollen or branched; zoospores 20 to 50, laterally biciliate, broadly reniform, measuring 9 to 10 μ in diameter upon encystment. Oogonia subspherical, echinulate, terminal or subterminal, also laterally or tangentially intercalary, 17 to 35 μ, average 26.4 μ, in diameter exclusive of the spines which are numerous, conical and acutely tipped, 3 to 7 μ, average 3.9 μ, long, and 1.5 to 3.5 μ, average 2.2 μ, in basal diameter; oogonia developing parthenogenetically in about 4 out of 5 cases. Antheridia lacking in many instances, when present usually diclinous, infrequently monoclinous, the terminal antheridial cell 12 to 25 μ, average 18 μ, long, and 5.5 to 8 μ wide, clavate and slightly crook-necked, often lobed by 2 to 3 transverse constrictions. Oospores aplerotic, single, 15 to 30 μ, average 23.1 μ, in diameter with a wall approximately 1.5 μ thick and containing a single reserve globule and refringent body.

Originally described from roots of *Pisum sativum* L., United States.

The contiguous sporangia of *Pythium oligandrum* are a distinctive feature of the species and readily distinguish it from other echinulate oogonial types with aplerotic oospores.

The oogonia of *Pythium oligandrum* are very similar to those of *P. anandrum;* both have conical, acute spines. The spines of *P. oligandrum* are from 3 to 7 μ, average 3.9 μ, in length and 1.5 to 3.5 μ, average 2.2 μ, in basal diameter, whereas the spines of *P. anandrum* are from 3 to 11 μ, average 7.1 μ, in length and 2 to 4 μ, average 2.8 μ, in basal diameter. The oogonial protuberances are more or less regularly arranged over the oogonium, differing considerably from the irregular placement of acantha in *P. irregulare.*

The antheridium of *Pythium oligandrum* is ordinarily diclinous with an inflated saccate antheridial cell which is closely applied to the oogonium. A

large percentage of the oogonia develop oospores in the absence of a visible antheridium; the species is, in this respect, analagous to *P. anandrum* in which there is no antheridium.

Pythium oligandrum and *P. anandrum* are quite different in their growth habits and temperature-growth relations; the maximum temperature for growth of *P. oligandrum* is 37° C. and between 31° and 34° C. for *P. anandrum*.

In addition to the original isolation of this species from *Pisum sativum* L. in the United States by Drechsler, it has been found on *Daucus carota* L., *Euphorbia pulcherrima* Willd., *Rheum rhaponticum* L., *Stipa* sp. and *Triticum aestivum* L. in the United States by the author, from *Viola tricolor* L. in England by Chesters, from *Prunus amygdalus* Stokes fruits in Cyprus by Nattrass (1937), from *Antirrhinum majus* L., *Cucurbita pepo* L., *Brassica oleracea* L. var. *capitata* L., and *Papaver rhoeas* L. in South Africa by Wager (1940); snapdragon and shirley poppy were originally reported by Wager (1931) as hosts for *Pythium* sp. cf. *artotrogus*, but transferred by him in 1940 to *P. oligandrum*.

52. PYTHIUM MEGALACANTHUM de Bary, Abhandl. Senckenb. Naturf. Ges. **12**: 19. 1881; Bot. Zeit. **39**: 539–544. 1881.

Pythium megalacanthum var. *callistephi* Tasugi and Siino, Ann. Phytopath. Soc. Japan **10**: 278–293. 1940.

Mycelium fine, branched, intracellular and intercellular. Sporangia formed in the epidermal cells of the host, or exogenously, acrogenous and intercalary, spherical to subspherical, frequently proliferous through continued growth of the sporangiophore, forming the secondary sporangium above the primary. Zoospores large, 4 to 5 μ to 18 to 20 μ, usually 12 to 15 μ, in size. Oogonia acrogenous or intercalary, spherical at first with a smooth surface which later became echinulate, exclusive of spines measuring 36 to 45 μ in diameter; spines 6 to 9 μ long, conical, usually acutely tipped. Antheridia diclinous, 1 or more to an oogonium. Oospores aplerotic, smooth and thick-walled, about 27 μ in diameter.

Saprophytic on vegetable debris, Germany.

Pythium megalacanthum differs from all other echinulate oogonial forms in possessing proliferous sporangia. The reports of Buisman (1927) and Diddens (1932) concerning a disease of flax, presumably caused by *P. megalacanthum*, state that the sporangia of the flax fungus are similar to those described by de Bary for *P. megalacanthum*. All attempts to induce zoospore formation and sporangial proliferation failed. Drechsler (1939), in a discussion of the flax parasite states that he also was unable to induce zoospore formation in this fungus. All attempts by the writer to secure zoospore formation and sporangial proliferation of the flax fungus likewise were unsuccessful. Nicolas and Aggery (1928) and Petri (1935) report observations concerning a fungus which was believed to be *P. megalacanthum* but do not mention whether they saw sporangial proliferation. Cejp (1931),

working with a culture of *P. megalacanthum* isolated from soil, describes the sporangia of his fungus as proliferous. An isolate identified by the writer as *P. megalacanthum* exhibited proliferous sporangia when agar blocks containing the fungus were irrigated with water.

Drechsler (1939) points out that the exact identity of the flax fungus is questionable, that until proliferous sporangia are observed specific assignment of the organism to *P. megalacanthum* is not possible. The writer concurs with this opinion, but believes that tentative identification of the fungus as *P. megalacanthum* is justifiable in view of the similarity of the sexual stage of the flax fungus to that of the referred species.

The reports of *Pythium megalacanthum* published subsequent to de Bary's description of the species, with the possible exception of Cejp's, do not present sufficient evidence to prove that the fungus referred to that binomial is actually identical with the species originally studied by de Bary.

The oogonia of *Pythium megalacanthum* resemble those of *P. mastophorum* and *P. polymastum;* however, the spines of these species are typically mammiform while those of *P. megalacanthum* are more or less conical, straight or slightly curved, with an obtuse to almost acute tip.

Pythium mastophorum and *P. polymastum* lack proliferous sporangia and are thus readily distinguished from *P. megalacanthum;* if proliferous sporangia fail to develop the species may usually be distinguished by the type of echinulation present.

Pythium megalacanthum is reported from the plants listed below:

Ananas comosus Merr. HAWAII: Sideris (1932).
Antirrhinum majus L. JAPAN: Tasugi and Siino (1940).
Calendula officinalis L. JAPAN: Tasugi and Siino (1940).
Callistephus chinensis Nees. JAPAN: Tasugi and Siino (1940).
Chrysanthemum sp. NETHERLANDS: Van Poeteren (1938).
Citrus sinensis Osbeck. ITALY: Petri (1935).
Erica regerminans L. UNITED STATES: Author.
Euphorbia pulcherrima Willd. UNITED STATES: Author.
Lactuca sativa L. JAPAN: Tasugi and Siino (1940).
Lepidium sativum L. ENGLAND: Salmon and Ware (1938). GERMANY: de Bary (1881b).
Linum usitatissimum L. GERMANY: Schilling (1928). NETHERLANDS: Buisman (1927); De Jonge (1933); Diddens (1932); Dorst (1938); Van der Meer (1928).
Lycopersicon esculentum Mill. JAPAN: Tasugi and Siino (1940). UNITED STATES: Author.
Papaver nudicaule L. UNITED STATES: Author.
P. rhoeas L. JAPAN: Tasugi and Siino (1940).
Pelargonium sp. NETHERLANDS: Van Poeteren (1938).
Petroselinum hortense Hoffm. FRANCE: Nicolas and Aggery (1928).
Primula sp. NETHERLANDS: Van Poeteren (1938).
P. obconica Hance: UNITED STATES: Author.
Soil. BOHEMIA: Cejp (1931). GERMANY: de Bary (1881b).
Todea africana Willd. GERMANY: de Bary (1881b).
Veronica hederaefolia L. GERMANY: Schröter (1889).
Zinnia elegans Jacq. JAPAN: Tasugi and Siino (1940).
Melon. FRANCE: Labrousse and Marcel (1934).

53. PYTHIUM ANANDRUM Drechsler, Jour. Wash. Acad. 20: 398–418. 1930.

Hyphae measuring 2 to 8 μ in diameter. Sporangia terminal, usually on long sporangiophores, sometimes later occupying a lateral position due to continued growth of the supporting branch, elongate, prolate ellipsoidal, 32 to 85 μ, average 50.4 μ, long and 18 to 40 μ, average 25.3 μ, wide, papillate, the apical papilla 3 to 5 μ long and 6 to 8 μ broad at base, occasionally proliferous, the subsequent sporangia usually produced beyond the primary; zoospores usually produced in sessile vesicle, 8 to 30, laterally biciliate, reniform, measuring 12 to 14 μ in diameter upon encystment. Oogonia subspherical, terminal, measuring 12 to 33 μ, average 28.3 μ, in diameter, exclusive of the numerous conical, acutely tipped spines which measure 2 to 11 μ, average 7.1 μ, in length and 1 to 4 μ, average 2.8 μ, in basal width; oogonia are constantly parthenogenetic. Antheridia lacking. Oospore aplerotic and apandrous, single, measuring 11 to 28 μ, average 24.4 μ, in diameter, provided with a wall approximately 1.6 μ thick and containing a single reserve globule and refringent body.

Originally described from *Rheum rhaponticum* L., United States.

Pythium anandrum is readily identified by its non-proliferous papillate sporangia, unique among echinulate oogonial congeners. The oogonia of *P. anandrum* and *P. oligandrum* are very similar, both having conical, narrow, acute spines; the contiguous sporangia of *P. oligandrum* are in sharp contrast with the prolate ellipsoidal sporangia of *P. anandrum*. The absence of antheridia also serves in segregating this species from *P. oligandrum*.

The minimum temperature for mycelial development of *Pythium anandrum* is low, 1° C., compared with 10° C. for *P. oligandrum*.

Pythium anandrum is known only in the United States from *Citrullus vulgaris* Schrad. fruits by Drechsler (1939), fruits of *Cucumis sativus* L. and roots of *Phaseolus vulgaris* L. by the author, *Rheum rhaponticum* L. crowns by Drechsler (1930a) and the author (1941b); and roots of *Spinacea oleracea* L. by the author.

54. PYTHIUM ECHINULATUM Matthews, Studies on the genus Pythium. 1931.

Hyphae measuring 2 to 8 μ in diameter. Sporangia spherical to cylindrical, terminal or intercalary, often catenulate, 3 or 4 in a series, measuring 10 to 30 μ, average about 20 μ, in diameter; zoospores or germ tubes are produced. Oogonia spherical to cylindrical, terminal or intercalary, measuring 14 to 30 μ, average about 24 μ, in diameter exclusive of the many spines 2 to 8 μ in length. Antheridia monoclinous, typically hypogynal, 1 to 4 per oogonium, usually 1. Oospores aplerotic, 14 to 24 μ, average about 20 μ, in diameter, 1 to 2 per oogonium, possessing a thick wall enclosing a single reserve globule and refringent body.

Originally described from soil in the United States.

There are several distinctive features in this species, particularly in its asexual stage. The sporangia are largely intercalary and very frequently catenulate, whereas in all other species possessing spiny oogonia spherical, intercalary, sporangia may be present but never arranged in a chain.

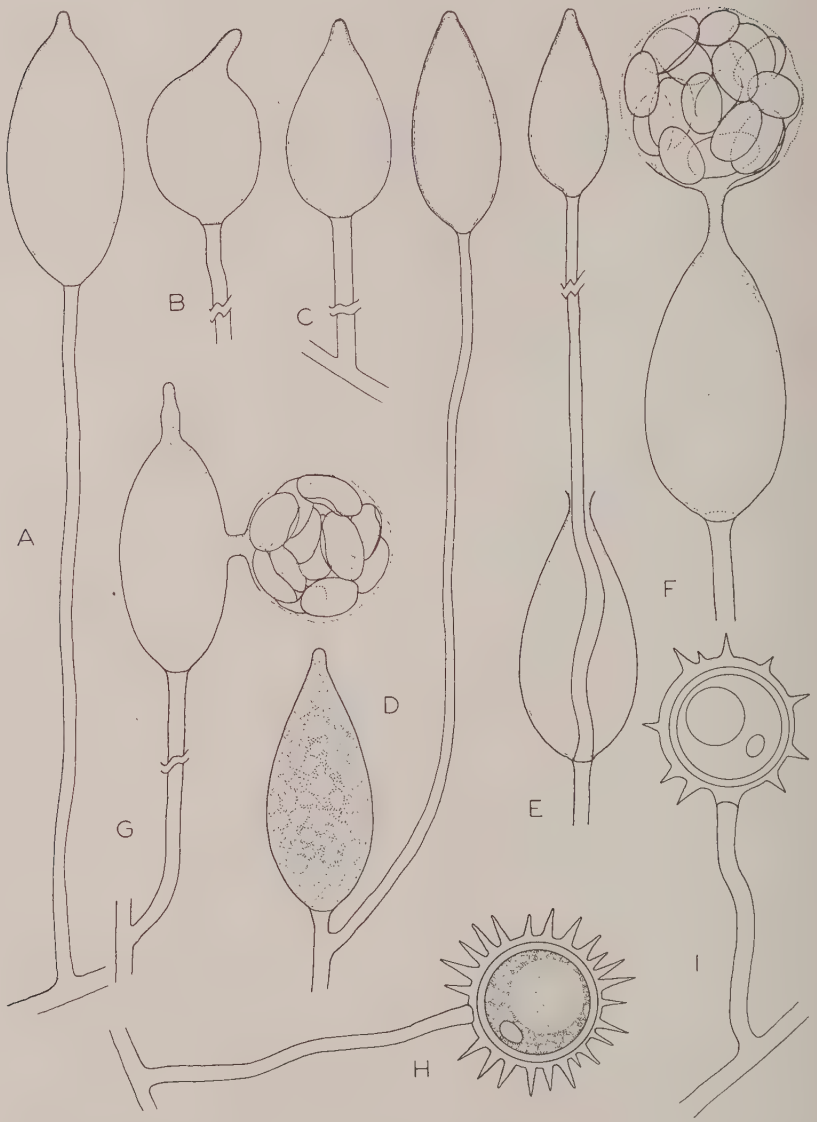

FIG. 16. *Pythium anandrum*. *A–E*, Various sporangial types. *A*, *C*, Typical shape. *B*, Sporangium of unusual occurrence, possessing a skewly beaked papilla. *D*, Secondary sporangium produced at the tip of a sporangiophore originating at the base of the primary sporangium. *E*, Typical sporangial proliferation. *F*, *G*, Zoospore formation. *G*, The apical emission tube has become nonfunctional, the secondary emission tube being formed in a lateral position. *F*, vesicle formation of the usual type. *H*, *I*, The sexual apparatus.

The oogonia of *Pythium echinulatum* resemble those of *P. oligandrum* and *P. anandrum* more than any other species, but differ in having spines with a relatively large basal diameter and an acuminate form rather than with a relatively small basal diameter and a conical form with an acute apex.

Hypogynal antheridia are usually present in *Pythium echinulatum;* they resemble those observed in *P. artotrogus* and *P. echinocarpum*, species lacking an asexual reproductive phase. This type of antheridium is not found in congeners possessing echinulate oogonia and an asexual reproductive phase.

A culture received as *Pythium echinulatum* proved to be more closely related to *P. acanthicum*. The growth habit and temperature-growth relations of this particular isolate are identical with those of *P. acanthicum*.

The species is known only from the original description and a single report from rotting *Viola tricolor* L. plants in the Netherlands by van Eek (1938).

55. PYTHIUM MASTOPHORUM Drechsler, Jour. Wash. Acad. **20**: 398–418. 1930.

Hyphae measuring 2 to 7.8 μ in diameter; appressoria moderately produced, knob-like, 8 to 12 μ in diameter at the expanded apex. Sporangia subspherical, smooth-walled, typically terminal, occasionally subterminal or apically intercalary, 17 to 38 μ, average 29.3 μ, in diameter; zoospores 3 to 14, reniform and laterally biciliate, measuring 12 to 14 μ in diameter upon encystment. Oogonia subspherical, typically terminal on branches 5 to 25 μ long, measuring 24 to 48 μ, average 35 μ, in diameter exclusive of the spiny protuberances 2 to 8 μ, average 5.2 μ, long and 2 to 6 μ, average 4.3 μ, wide at the base, conical or more typically mammiform, the apex usually attenuated and papillate. Antheridia diclinous, usually terminal but infrequently intercalary, usually somewhat lobate, 7 to 15 μ wide and 16 to 28 μ long, making broad apical contact with the oogonium, frequently the antheridial stalk becomes intimately associated with the oogonial stalk, usually 1 per oogonium. Oospores aplerotic, 20 to 44 μ, average 28.9 μ, in diameter, provided with a wall 1.4 to 2.3 μ, average 1.8 μ, thick and containing a single reserve globule and refringent body; germination by means of zoospores or germ tubes.

Originally described from *Bellis perennis* L., United States.

The description given above adequately delineates the species but does not indicate its relationships or distinguishing characteristics.

The oogonia of *Pythium mastophorum*, *P. polymastum*, and *P. megalacanthum* are very similar. Those of *P. megalacanthum* have conical, obtuse or slightly pointed spines, while the spines of *P. mastophorum* and *P. polymastum* are mammiform. The average diameter of the oogonia of *P. mastophorum* is 35 μ compared with an average of 45 μ in *P. polymastum;* the oospores are proportionally smaller, 29 μ and 35 μ in diameter, respectively.

Pythium mastophorum and *P. polymastum* are readily distinguished by their sporangia and type of evacuation tube. The sporangia of *P. mastophorum* are largely terminal, sometimes intercalary, spherical and regular in outline, and develop an evacuation tube that is contorted, bearing one or

several branched, vegetative prolongations; the sporangia of *P. polymastum* are largely intercalary, irregular in contour due to the presence of dome-like protuberances, or composed of 2 or 3 lobed communicating parts, and develop a straight unbranched evacuation tube.

The mammiform spines distinguish *Pythium mastophorum* from *P. irregulare*, *P. echinulatum*, and *P. anandrum*. The typically diclinous antheridium of *P. mastophorum* differs decidedly from the typically monoclinous antheridia of *P. irregulare*, hypogynous antheridium of *P. echinulatum* and the absence of antheridia on *P. anandrum*.

This species is known from *Bellis perennis* L. by Drechsler (1930a, 1939) and from *Calceolaria crenatiflora* Cav. by the author, both in the United States.

56. PYTHIUM POLYMASTUM Drechsler, Jour. Wash. Acad. **20**: 398–418. 1930.

Hyphae measuring 2.5 to 9.5 μ in diameter; appressoria usually lacking. Sporangia usually subspherical, often noticeably oblate, usually intercalary, or infrequently terminal and then later becoming lateral due to prolongation of the sporangiophore, measuring 20 to 36 μ, average 30 μ, in diameter, sometimes irregular in shape due to 1 or more dome-shaped protuberances or even composed of 2 or 3 subspherical parts fused into a lobate structure; zoospores 2 to 12, formed in a vesicle arising indiscriminately from the sporangium, reniform and laterally biciliate, measuring 14 to 17 μ in diameter upon encystment. Oogonia subspherical, typically terminal on short lateral branches, also lateral and sessile, measuring 29 to 67 μ, average 45.6 μ, in diameter exclusive of the conical or mammiform spines 1 to 10 μ, average 5.5 μ, long, and 2.5 to 6.5, average 4.5 μ, wide at base. Antheridia diclinous, 1 to 4 per oogonium, usually terminal, sometimes intercalary, lateral or sessile on the parent filament, the antheridial cell broadly saccate, cylindrical or barrel-shaped, lobate or with diverticulate protuberances, 20 to 43 μ, average 27 μ, long and 12 to 21 μ, average 15 μ, wide, making broad apical oogonial contact. Oospores aplerotic, 25 to 42 μ, average 35.3 μ, in diameter, with a wall about 1.6 μ thick containing a single reserve globule and refringent body; germination not observed.

Originally described from *Lactuca sativa* L., United States.

The observations of the writer concur with Drechsler's description of the fungus.

Pythium polymastum exhibits resemblances to *P. mastophorum* and *P. megalacanthum;* all possess fairly large echinulate oogonia and aplerotic oospores. The spines of *P. polymastum* and *P. mastophorum* are typically mammiform, while those of *P. megalacanthum* are conical and obtuse or papillate.

The sporangium of *P. polymastum* is non-proliferous and non-papillate, distinguishing this species from *P. megalacanthum* and *P. anandrum*. A peculiar characteristic of the sporangium of *P. polymastum* is its tendency to become irregular in contour and often even lobate composed of two or three subspherical parts fused together. The sporangium of *P. mastophorum*

is regular in contour and devoid of protuberances. The evacuation tube of *P. polymastum* is fairly short, straight and unbranched, further distinguishing the species from *P. mastophorum* in which the evacuation tube is longer, more or less contorted and frequently bears several branched vegetative prolongations. The size of the oogonia may be used here to advantage, those of *P. mastophorum* averaging 35 μ in diameter while the oogonia of *P. polymastum* average 45.6 μ in diameter.

In addition to the reports of Drechsler (1930a, 1939) isolating this fungus from *Lactuca sativa* L., the author has obtained it from roots of *Bellis perennis* L., *Daucus carota* L. and *Euphorbia pulcherrima* Willd., all in the United States.

57. Pythium irregulare Buisman, Med. Phytopath. Lab. 11: 1–51. 1927.

Hyphae measuring 2.6 to 7.9 μ in diameter. Sporangia of various shapes, mostly spherical to obovate, but sometimes ellipsoidal, pyriform and truncate, terminal or intercalary, measuring 10 to 26.7 μ, average 18.0 μ, in diameter; zoospores seldom produced, about 8 μ in diameter upon encystment. Oogonia spherical to limoniform, measuring 9.6 to 28.3 μ, average 17.8 μ, in diameter, usually intercalary though also terminal, of irregular contour, fairly smooth or undulant to definitely irregularly echinulate, the spines varying in shape but usually of broad base and acuminate apex, straight or contorted. Antheridia typically monoclinous, occasionally diclinous, 1 to 4, usually 1 to 2, per oogonium, stalked, the antheridial cell short, clavate and slightly crook-necked, making apical contact with the oogonium. Oospores aplerotic, measuring 8.1 to 25.2 μ, average 15.4 μ, in diameter, wall about 1.4 μ thick and containing a single reserve globule and refringent body.

Originally described from *Cucumis sativa* L., *Lupinus* sp. and *Pisum sativum* L., the Netherlands.

The sporangia of *Pythium irregulare* vary in shape from spherical to subspherical, elliptical to ovoid, pyriform to truncate, and are either acrogenous or intercalary, probably of more diverse shape than any other species of the genus.

The sexual stage of *Pythium irregulare* is analogous to that of *P. debaryanum*, differing principally in the presence of oogonial protuberances in the former. The spines of *P. irregulare* are few to numerous, always of irregular lengths and irregularly arranged on the oogonium. The spines may be dome-shaped, conical, papillate or curved-digitate, septate or non-septate but always with a blunt tip. The oogonia are both intercalary and acrogenous. The antheridia are usually monoclinous, occasionally diclinous; the antheridial cell is stalked, small in relation to the oogonium, slightly inflated, clavate, crook-necked, the apex slightly applied to the oogonial wall. The antheridia vary from 1 to 5 in number, usually 2 to 3, per oogonium.

The oospore is aplerotic, thin-walled, filled with dense, granular protoplasm containing a single, small, reserve globule and a prolate ellipsoidal refringent body.

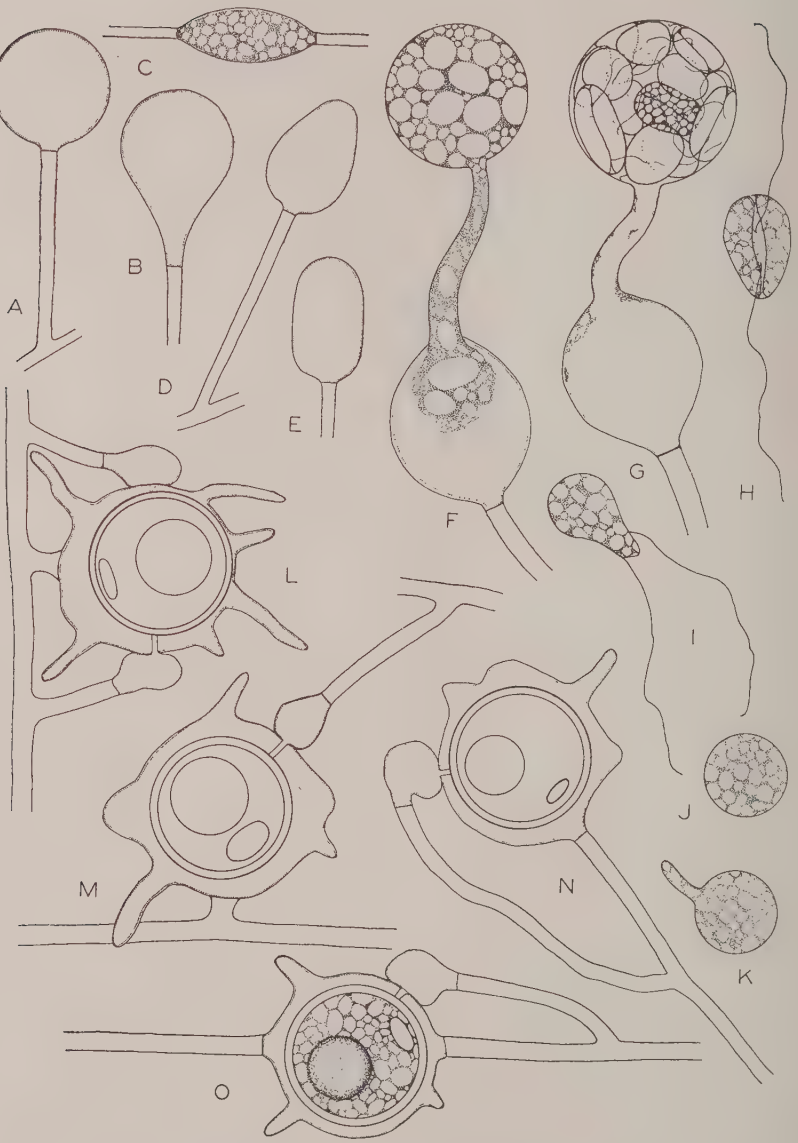

FIG. 17. *Pythium irregulare*. *A–E*, Sporangial types of usual occurrence. *F*, *G*, Zoospore formation. *F*, The contents of the sporangia flow through the emission tube into the apical, rounded vesicle; the vesicle contents are as yet undifferentiated. *G*, The vesicle contents have become differentiated into zoospores. These will be liberated by the subsequent dissolution of the vesicle wall. *H*, Typical motile zoospores. *I*, Zoospores beginning quiescence. *J*, Zoospores at encystment. *K*, Zoospores initiate germination. *L–O*, Various orientations of the sexual apparatus.

The growth habit and temperature-growth relations of *Pythium irregulare* are very similar to those of *P. debaryanum*, *P. ultimum*, and many other species and cannot be used as adjuncts in identifying it.

Agropyron cristatum (L.) Gaertn. UNITED STATES: Fischer *et al.*, (1942).
Agrostis stolonifera L. NETHERLANDS: Van Luijk (1934a, 1938a).
Ananas comosus Merr. HAWAII: Parris (1940); Sideris (1932); Sideris and Paxton (1931).
Antirrhinum majus L. ENGLAND: Vanterpool. UNITED STATES: Middleton (1938); Nance (1939).
Anthoceros sp. UNITED STATES: Matthews (1931).
Atropa belladonna L. UNITED STATES: Middleton (1941a).
Avena sativa L. UNITED STATES: Melhus, Reddy and Buchholtz (1939); Sprague.
Azalea obtusum Planch. UNITED STATES: Author.
Bouteloua gracilis (H.B.K.) Lag. UNITED STATES: Sprague.
Bromus inermis Leyss. UNITED STATES: Fischer *et al.* (1942).
B. tectorum L. UNITED STATES: Fischer *et al.* (1942).
Cajanus cajan Millsp. HAWAII: Parris (1940). Sideris (1932).
Canavalia ensiformis DC. HAWAII: Parris (1940). Sideris (1932).
Carica papaya L. UNION SOUTH AFRICA: Wager (1931, 1932a, 1940).
Chamaecyperis lawsoniana Parl. UNITED STATES: Author.
Citrullus vulgaris Schrad. UNITED STATES: Younkin (1938); Younkin and Melhus (1939, 1940); Author.
Citrus sp. UNION SOUTH AFRICA: Wager (1931, 1940).
Cucumis sativus L. NETHERLANDS: Buisman (1927).
Elymus junceus Fisch. UNITED STATES: Fischer *et al.* (1942).
Festuca duriuscula L. NETHERLANDS: Van Luijk (1934a, 1938a).
F. elatior L. UNITED STATES: Fischer *et al.* (1942).
Helianthus annuus L. HAWAII: Parris (1940); Sideris (1932).
Hordeum bulbosum L. UNITED STATES: Sprague.
Ipomoea batatas Lam. HAWAII: Parris (1940); Sideris (1932).
Linum usitatissimum L. NETHERLANDS: Diddens (1932).
Lolium annuum L. var. *westerwoldicum*. NETHERLANDS: Van Luijk (1938a).
Lupinus sp. NETHERLANDS: Buisman (1927).
Phaseolus aureus Roxb. HAWAII: Parris (1940); Sideris (1932).
Picea abies Karst. UNITED STATES: Author.
Pimelea ferruginea Labill. UNITED STATES: Author.
Pinus resinosa Ait. UNITED STATES: Roth and Riker (1942); Author.
P. rigida Mill. UNITED STATES: Author.
Pisum arvense L. UNITED STATES: Weimer (1940).
P. sativum L. NETHERLANDS: Buisman (1927).
Primula obconica Nance. UNITED STATES: Middleton (1938); Nance (1939).
P. sinensis Lindl. UNITED STATES: Author.
Ranunculus asiaticus L. UNITED STATES: Tompkins and Middleton (1939, 1942).
Saccharum officinarum L. UNITED STATES: Rands and Dopp (1938b); Stevenson and Rands (1938).
Spinacea oleracea L. UNITED STATES: Nance (1940).
Triticum aestivum L. UNITED STATES: Sprague.
Tritonia sp. UNITED STATES: Author.
Vicia sp. UNITED STATES: Weimer (1940).
V. faba L. HAWAII: Parris (1940); Sideris (1932).

58. PYTHIUM UNDULATUM Petersen, Bot. Tidssk. **29**: 345–440. 1909; Ann. Mycol. **8**: 494–560. 1910.

Mycelium within the substrate difficult to distinguish, extramatrical mycelium rarely branched, more or less undulating, long, measuring 3 to 6 μ in diameter. Sporangia acrogenous, ellipsoidal, sometimes with a small apical papilla, measuring 130 μ long and 50 μ wide, proliferous, the subse-

quent sporangia usually formed within the primary one; zoospores laterally biciliate, reniform, measuring 15 to 20 μ in diameter upon encystment, formed in a sessile, apical vesicle. Sexual reproduction not observed.

Originally described from leaves of *Nymphaea alba* L. and *Nuphar luteum* Sibth. and Sm., Denmark.

The sporangia are proliferous, a new sporangium being formed within or beyond the old one. Secondary sporangia formed exogenously are borne on relatively short stalks. Occasionally sporangia are formed laterally at the base of an acrogenous primary sporangium. Regardless of position of sporangium, the vesicle is sessile, arising from the papilla.

Pythium undulatum may be distinguished from *P. intermedium* and *P. elongatum* by its proliferous habit which is typical also in *P. diacarpum*, and *P. carolinianum*. *P. undulatum* differs from these species in its vesicle which is sessile upon the sporangium, while those of *P. diacarpum* and *P. carolinianum* are stalked.

In addition to *Nymphaea alba* L. and *Nuphar luteum*, Petersen lists this species from old fruits of *Iris* sp. and vegetable debris (". . . branches of trees . . .") in Denmark, Dissmann (1927) isolated *Pythium undulatum* from leaves of *Nymphaea candida* Presl. in Bohemia and Matthews (1931) from soil in the United States.

59. Pythium carolinianum Matthews, Studies on the genus Pythium. 1931.

Hyphae fine, measuring 1 to 4 μ in diameter. Sporangia typically acrogenous, intercalary, spherical to elongate, measuring 20 to 30 μ, average 25 μ, in diameter, with a well developed apical papilla, proliferous with the secondary sporangia formed inside or out of the primary ones; zoospores numerous, formed in a stalked vesicle, laterally biciliate and reniform, measuring 8 to 10 μ in length. Sporangia sometimes germinate by the production of germ tubes.

Originally described from *Spirogyra* sp., United States.

A single isolate of this species was observed by the writer; *Pythium carolinianum* is readily identified. The shape of the sporangium and the position of the vesicle separate *P. carolinianum* from *P. undulatum*. The sporangium of *P. carolinianum* is spherical to elliptical with the vesicle borne on a short stalk, while the sporangium of *P. undulatum* is prolate ellipsoidal and bears a sessile vesicle. The sporangia of both species are proliferous and papillate, distinguishing them from *P. diacarpum* which is a proliferous form without papillae. *P. intermedium* and *P. elongatum* are not proliferous species and cannot be confused with *P. carolinianum*.

Pythium carolinianum is known only from *Spirogyra* sp. (Matthews) and vegetable debris (Author) in the United States.

60. Pythium diacarpum Butler, Mem. Dept. Agr. India 1^5: 1–160. 1907.

Hyphae very slender, less than 1.5 μ in diameter, sparingly branched. Sporangia acrogenous and spherical, approximately 30 μ in diameter, capable

of proliferation. Evacuation tube long, several times the length of the sporangium, often wavy or helicoid, about 2 to 3 μ in diameter; zoospores infrequently formed exogenously though typically within the vesicle, capable of repeated emergence. Sexual reproduction not observed.

Saprophytic on vegetable debris, Germany.

The non-papillate sporangium of *Pythium diacarpum* readily distinguishes the species from the allied proliferous forms, *P. undulatum* and *P. carolinianum*. The sporangium of *P. diacarpum* is spherical and borne on a fine hypha, 1.5 μ in diameter. The evacuation tube produced at the initiation of zoospore formation is characteristically twice the diameter of the sporangiophore. At the tip of the evacuation tube an urn-shaped vesicle forms which remains distinguishable for some time; none of the allied species, *P. undulatum*, *P. carolinianum*, *P. intermedium*, or *P. elongatum* exhibit a long evacuation tube of this type. The proliferous habit of *P. diacarpum* further separates it from *P. intermedium* and *P. elongatum*.

This species is known only from the original report.

61. PYTHIUM INTERMEDIUM de Bary, Bot. Zeit. **39**: 553–558. 1881.

Artotrogus intermedius Atkinson, Cornell Agr. Exp. Sta. Bull. 94: 233. 1895.

Mycelium branched, 2 to 6 μ in diameter, coenocytic when young, septate when mature. Sporangia spherical, 18 to 24 μ in diameter, catenulate, often up to 13 in a series, the sporangia sessile or separated by short stalks. Sexual reproduction unknown.

Parasitic on prothallia of *Ceratopteris*, *Equisetum* and *Todea* and saprophytic on *Amaranthus* and *Lepidium* seedlings.

Pythium intermedium is readily identified by its catenulate sporangia. These are usually spherical when stalked and frequently pyriform when sessile, the tapered part arising from the sporangium below. The terminal sporangia are occasionally deciduous when more than 10 are arranged in a series. Germination is usually accomplished by the production of zoospores in a vesicle on a short evacuation tube; germ tubes are occasionally formed.

The intercalary sporangia of *Pythium carolinianum* are sometimes regarded as catenulate and may possibly be mistaken for those of *P. intermedium;* however, *P. carolinianum* is distinguished from *P. intermedium* by its proliferous, papillate sporangia.

Pythium intermedium is known from the following list of plants: *Agrostis stolonifera* L. in the Netherlands by van Luijk (1938a); *Amaranthus* sp. in Germany by de Bary (1881); *Aquilegia vulgaris* L. and *Arabis alpina* L. in the Netherlands by Meurs (1928); *Begonia lloydii* (Hort. name) and *B. tuberhybrida* Voss in the United States by Middleton (1938, 1942) and Nance (1939); *Ceratopteris* sp. in Germany by de Bary (1881); *Chrysanthemum morifolium* Ram. in the Netherlands by Buisman (1927); *Equisetum* sp. in Germany by de Bary (1881); Fern prothallia in the United States by Atkinson (1895); *Festuca duriuscula* L. in the Netherlands by van Luijk (1938a);

Fragaria vesca L., *Godetia willdenowiana* Spach. and *Hesperis matronalis* L. in the Netherlands by Meurs (1928); *Lepidium* sp. in Germany by de Bary (1881); *Linum usitatissimum* L. in the Netherlands by Diddens (1932); *Lolium annuum* L. var. *westerwoldicum* in the Netherlands by van Luijk (1938a); *Lupinus angustifolius* L. in Germany by Schultz (1939); *Pelargonium* sp. in the Netherlands by Buisman (1927); *Phaseolus vulgaris* L. and *Pisum sativum* L. in the Netherlands by Meurs (1928); *Pyrus communis* L. in Belgium by Marchal and Marchal (1921), *P. Malus* L. in Germany by Schultz (1939); *Ricinus communis* L. in the United States by the author. Soil in England, France and Germany by Butler (1907); *Todea* sp. in Germany by de Bary (1881); *Tulipa gesneriana* L. in the United States by the author; *Ulmus campestris* L. var. *latifolia* in the Netherlands by Westerdijk and Buisman (1929) and Westerdijk, Ledeboer and Went (1931); *Viola tricolor* L. in the Netherlands by Meurs (1928) and van Eek (1938).

62. Pythium elongatum Matthews, Studies on the genus Pythium. 1931.

Hyphae measuring 2 to 4 μ in diameter, branched. Sporangia terminal or intercalary, spherical, pyriform, cylindrical or curved, when spherical measuring 12 to 50 μ, when cylindrical measuring up to 65 μ long; zoospores produced in a vesicle borne on a very long evacuation tube, laterally biciliate, reniform, about 6 μ wide and 10 to 12 μ long. Sporangia also germinate by means of germ tubes. Sexual reproduction not observed.

Originally isolated from soil, United States.

Pythium elongatum is one of two species lacking sexual reproduction that does not have a proliferous or catenulate sporangial habit. The absence of sporangial proliferation distinguishes the species from *P. undulatum*, *P. carolinianum*, and *P. diacarpum;* the absence of catenulate sporangia separates the species from *P. intermedium*.

The fungus is known only from the original report.

63. Pythium sclerotеichum Drechsler, Jour. Agr. Res. **49**: 881–890. 1934.

Hyphae branched, measuring 2.5 to 7 μ in diameter; terminal, clavate, appressoria present measuring 5 to 12 μ in diameter. Sporangia unknown. Oogonia spherical, typically acrogenous though sometimes intercalary, measuring 16 to 32 μ, average 23.8 μ, in diameter, the wall sturdy and smooth, measuring 0.5 to 1.2 μ, average 0.9 μ, thick, the septum or septa usually inserted beyond the oogonial contour. Antheridia monoclinous or diclinous, terminal, 1 to 5, usually 3, per oogonium frequently 2 cells to a stalk, the cell clavate, crook-necked, 9 to 16 μ long and 4 to 7 μ wide, the blunt apical end making narrow contact or broadly appressed to the oogonial wall, the antheridial branches sometimes containing a number of septa and constricted at intervals by relatively deep, transverse, dorsal furrows, the branches together with their frequent vegetative prolongations extensively and intimately wrapped about the oogonium. Oospore aplerotic, distinctly yellowish, measuring 11 to 26 μ, average 18.7 μ, in diameter, the wall thin, 0.8 to 1.4 μ, average 1.1 μ, thick and containing a single reserve globule and refringent body.

Originally described from roots of *Ipomoea batatas* Lam., United States.

Pythium scleroteichum is one of a group of species ascribed to the genus *Pythium* despite the absence of sporangia. The type and method of sporangial germination is a generic characteristic, and there may be objections to the inclusion of a species not exhibiting sporangial habits typical of *Pythium*. However, this species and other members of the group are included in the genus on the basis of their mycelial character, type of oogonium, antheridium, and oospores.

An oogonium devoid of echinulations readily distinguishes *Pythium scleroteichum* from *P. acanthophoron*, *P. artotrogus*, and *P. echinocarpum*. The antheridia resemble somewhat those of *P. adhaerens* and *P. periilum* in that the several antheridial cells arise from a single antheridial branch. The antheridia differ, however, in not being restricted in origin to a single monoclinous or diclinous branch, often arising from separate parent hyphae without close mycelial connection. As in *P. periilum*, the antheridia and vegetative ramifications of the antheridial stalk frequently envelop the oogonium intimately and extensively. The antheridial branches are sometimes constricted by fairly deep, transverse fissures.

As pointed out by Drechsler (1934b) the oospores of this species degenerate in culture unless the pH of the nutrient agar substrate ranges between 4.5 and 5.0.

The temperature-growth relations of this fungus may be used as an adjunct to its morphological identification.

This species is known only from sweet-potato, *Ipomoea batatas* Lam., in the United States, originally from a study of mottle necrosis by Harter and Whitney (1927b); it was not until 1934 that a description of the fungus was given by Drechsler.

64. PYTHIUM ARTOTROGUS (Mont.) de Bary, Abhandl. Senckenb. Naturf. Ges. **12**: 225–340. 1881.

Artotrogus hydnosporus Montagne, Gard. Chron. **1845**: 640. 1845; Jour. Roy. Hort. Soc. **1**: 9–34. 1846.
Pythium hydnosporum (Mont.) Schröter in Engl. & Prantl, Nat. Pfl. **1**: 104–105. 1897.
Pythium artotrogus var. *macracanthum* Sideris, Mycologia **24**: 14–61. 1932.

Hyphae branched, measuring 2.6 to 7.8 μ in diameter. Sporangia lacking. Oogonia spherical, usually intercalary though also acrogenous, measuring 18 to 27 μ in diameter, wall conspicuously echinulate. Antheridia typically hypogynous. Oospores aplerotic, 15 to 24 μ in diameter.

Originally described from *Solanum tuberosum* L., France.

The first description of the species by Montagne was incorporated in an editorial by Berkeley in 1845. A year later, Montagne gave the fungus a Latin diagnosis which was included in an article on potato blight by Berkeley. De Bary (1876) observed *Pythium artotrogus* in a diseased potato tuber and noted the similarity of *Artotrogus* and *Pythium* in his study of the potato blight fungus, *Phytophthora infestans*. It was not until later (1881)

that he concluded that the two genera were synonymous and transferred *Artotrogus hydnosporus* to the genus *Pythium* as *P. artotrogus*. Fischer (1892) in his treatment of the genus concurs with de Bary on this point. Schröter (1897), however, though recognizing the synonymity of the two, transferred *A. hydnosporus* to *P. hydnosporum*, disregarding the usual practice of transferring the invalid generic nomen to specific rank in the valid genus.

A study of the species more complete than that by Montagne is presented by Butler (1907). Sporangia are unknown. Oogonia are spherical, 18 to 27 μ, average 22.4 μ, in diameter, acrogenous or intercalary. Oogonial protuberances are conical, 2.7 to 8.3 μ long and about 1.8 μ wide in basal diameter, tapering to an acute apex. The antheridium is hypogynous, rarely sessile adjacent to the oogonium. Oospores are aplerotic and smooth walled. The oospore frequently germinates by the production of a branched hypha.

Acuminate spines and the hypogynous antheridium distinguish *Pythium artotrogus* from *P. acanthophoron*. The absence of monoclinous and diclinous antheridia distinguish *P. artotrogus* from *P. echinocarpum*.

Sideris described *Pythium artotrogus* var. *macracanthum* as a new variety stating, ". . . it differs from *P. artotrogus* in having some epigynous antheridia, in the greater length of the spines of its oospores and the greater amount of aerial mycelium produced in culture media." Epigynous antheridia, monoclinous and adjacent to the oogonium as sessile, inflated, clavate structures, are not unique to the new variety. Its spines are conical, acuminate, 7.5 to 10 μ long and 1.0 to 1.5 μ in basal diameter compared with the conical, acuminate, 2.7 to 8.3 μ long and about 1.8 μ basal diameter of the species. Further, Sideris states erroneously that the oospores are echinulate; the oogonia are echinulate and the oospores smooth. The differences distinguishing the variety from the species do not seem adequate to maintain it as a valid nomen.

Pythium artotrogus is known from the following hosts:

Ananas comosus Merr. HAWAII: Parris (1940); Sideris (1932); Sideris and Paxton (1931).
Apium graveolens L. var. *dulce* DC. ENGLAND: Stirrup and Ewan (1931).
Arabis alpina L. NETHERLANDS: Meurs (1928).
Brassica oleracea L. var. *botrytis* L. GERMANY: Kryopoulus (1916).
Cajanus cajan Millsp. HAWAII: Parris (1940); Sideris (1932).
Canavalia ensiformis DC. HAWAII: Parris (1940); Sideris (1932).
Ipomoea batatas Lam. HAWAII: Parris (1940); Sideris (1932).
Lycopersicon esculentum Mill. HUNGARY: Moesz (1938).
Nymphaea candida Presl. BOHEMIA: Dissmann (1927).
Panicum purpurascens Raddi. HAWAII: Parris (1940); Sideris (1932).
Phaseolus vulgaris L. HAWAII: Parris (1940); Sideris (1932).
Pinus banksiana Lamb. UNITED STATES: Gravatt (1925); Hartley (1921).
P. nigra Arn. var. *austriaca* Aschers. and Graebn. NETHERLANDS: Ten Houten (1939).
P. ponderosa Dougl. UNITED STATES: Hartley (1921).
P. resinosa Ait. UNITED STATES: Gravatt (1925); Hartley (1921).
Pseudotsuga taxifolia Britt. NETHERLANDS: Ten Houten (1939).
Raphanus sativus L. SWEDEN: Palm (1934).
Saccharum officinarum L. HAWAII: Parris (1940); Sideris (1932). UNITED STATES: Edgerton and Moreland (1921); Stevenson and Rands (1938).

Solanum tuberosum L. ENGLAND: Smith (1876). FRANCE: Montagne (1845, 1846). GERMANY: de Bary (1876, 1881b). INDIA: Butler (1907); Butler and Bisby (1931); Sydow and Butler (1907).
Spinacea oleracea L. NETHERLANDS: Meurs (1928).
Vigna sinensis Endl. HAWAII: Parris (1940).
Viola tricolor L. NORWAY: Solberg (1926).
Water. UNITED STATES: Matthews (1931).

Wager (1931) refers an isolate from *Antirrhinum majus* L. and *Papaver rhoeas* L. to this species, later (1940) placing the fungus under the binomial *Pythium oligandrum*.

65. PYTHIUM ECHINOCARPUM Ito & Tokunaga, Jour. Fac. Agr. Hokkaido Imper. Univ. **32**: 201–233. 1933.

Hyphae slender, 1.2 to 4.8 μ in diameter. Sporangia unknown. Oogonia terminal or intercalary, spherical, measuring 15 to 24 μ in diameter exclusive of the pointed, conical spines 4 to 9 μ long and 1.5 μ in basal diameter. Antheridia monoclinous, or diclinous, rarely hypogynous, single or rarely 2 per oogonium, when not hypogynous, clavate elongate and usually crook-necked, when hypogynous cylindrical and rarely inflated. Oospores aplerotic, single, 13 to 21 μ in diameter, the wall thin, 0.8 to 1.2 μ thick; germination not observed.

Originally described from seedlings of *Oryza sativa* L., Japan.

Cultures of this species were not available for study; the discussion is based on the material presented in the original article from which the description is taken.

The oogonia of *Pythium echinocarpum* are very much like those of *P. artotrogus;* they are both spherical, either terminal or intercalary, the spines of similar dimension and both conical and acutely tipped. The pointed spines of *P. echinocarpum* distinguish it from *P. acanthophoron* which possesses obtusely tipped spines. The oospores of the three species are all aplerotic. The commonly monoclinous or diclinous antheridia of *P. echinocarpum* separates the species from *P. artotrogus* which possesses hypogynous antheridia. Further study may prove the species to be synonymous with *P. artotrogus*.

This species is known only from the original description and the report of Darker (1940) stating its occurrence on *Oryza sativa* L. seedlings in Japan.

66. PYTHIUM ACANTHOPHORON Sideris, Mycologia **24**: 14–61. 1932.

Hyphae irregular, slightly dendroid, measuring 3 to 7 μ in diameter. Sporangia unknown. Oogonia spherical, acrogenous or intercalary, measuring 20 to 30 μ in diameter exclusive of the obtusely tipped spines (Sideris = 5 to 7 μ long). Antheridia monoclinous or diclinous, slightly curved, clavate, making broad oogonial contact, 10 to 20 μ long and 4 to 8 μ wide. Oospore aplerotic, 15 to 25 μ in diameter, the wall 1.5 μ thick.

Originally described from *Ananas comosus* Merr., Hawaii.

Sideris erroneously described *Pythium acanthophoron* as having smooth oogonia and spiny oospores. An authentic culture of this fungus studied

had spiny oogonia and smooth oospores. The oogonial protuberances are conical, usually 2.5 μ long and 1.7 μ in basal diameter, with an obtuse or blunt tip. The antheridia are mostly monoclinous, rarely diclinous, borne on a relatively short antheridial stalk. The antheridial cell is somewhat saccate and appressed to the oogonium.

Pythium acanthophoron and *P. acanthicum* are similar in size, shape, character of spines and type of antheridia, though these are more clavate and crook-necked in *P. acanthicum;* they differ decidedly, however, in the type of oospores, aplerotic in *P. acanthophoron*, plerotic in *P. acanthicum*. The conical, obtuse spines of *P. acanthophoron* separate this species from *P. artotrogus* and *P. echinulatum* both of which have acute spines.

The pulvinate growth habit of *P. acanthophoron* readily distinguishes it from *P. acanthicum*, which has a cumulous growth habit. *P. acanthophoron* is unique among the species studied in its failure to grow at temperatures below 13° C.

This species is known only from Hawaii on *Ananas comosus* Merr.

DOUBTFUL AND INVALID SPECIES

A number of the *Pythium* spp. reported here have previously been designated as doubtful by other authors, particularly Butler (1907) and Matthews (1931). A few are newly presented and the reasons given for their inclusion here. With the exception of *nomina nuda*, the larger number of entries are designated doubtful in the absence of adequate description and observation since their original presentation.

PYTHIUM ACTINOSPHAERII Brandt, Monatsb. K. Preuss. Akad. Wiss., Berlin, **1881**: 399. 1881.

Fischer (1892) believes this organism not to be a *Pythium;* Butler (1907) believes it to be a *Saprolegnia* sp. Zopf (1890) states that *P. actinosphaerii* was incorrectly described as a new species and should now be referred to *Actinosphaerium Eichhornii* Brandt; Zopf gives no morphologic discussion of the organism.

PYTHIUM AKANENSE Tokunaga, Trans. Sapporo Nat. Hist. Soc. **12**: 119–123. 1932.

The description of this fungus would indicate that it probably should be referred to *Pythium monospermum* rather than be maintained as a new and valid species. Information regarding the disposition of the antheridium is not given. The only differences between *P. akanense* and *P. monospermum* seems to be in the thickness of the oospore wall, a criterion which should not be used as the sole factor in specific segregation. Until the fungus has been observed and further studied it seems desirable to consider it a doubtful species, possibly synonymous with *P. monospermum*. This fungus is recorded from *Aegagropila sauteri* (Nees) Kütz. in Japan by Tokunaga, Ito and Tokunaga (1935) and Darker (1940); Tokunaga also reports the fungus able to infect *Cladophora* sp. upon inoculation.

PYTHIUM CHAMAIHYPHON Sideris, Mycologia **24**: 14–61. 1932.

This species was presumably transferred to *Pythium polycladon* as a variety of it. Since the inclusion of *P. polycladon* in *P. vexans* the taxonomic status of *P. chamaihyphon* has been doubtful.

PYTHIUM CHARACEARUM de Wildeman, Ann. Soc. Belg. Micros. **20**: 107–136. 1896.

Described as a new species on oogonia of *Chara* sp. collected in Switzerland. Acrogenous oogonia of unknown size, one to four antheridia of unknown origin and aplerotic oospores 20 to 30 μ in diameter are described; the asexual apparatus was not observed. The fungus has not been observed subsequent to its description. Until a more detailed diagnosis of this species is presented it must be considered of doubtful validity.

PYTHIUM CHLOROCOCCI Lohde, Tagebl. Versamm. Deutsch. Naturf. Aerzte, Breslau, **47**: 203. 1874.

The description presented is too meager and incomplete to permit identification of the species.

PYTHIUM CIRCUMDANS (Lohde) Fischer, Tagebl. Versamm. Deutsch. Naturf. Aerzte, Breslau, **47**: 203. 1874.

This species, although referred to as *Lucidium circumdans*, is probably a species of *Pythium*, Fischer (1892) transferring it to this genus and including it under *P. debaryanum*. Butler (1907) does not agree with Fischer's interpretation. On the basis of the imperfect description it would appear best to consider the species of doubtful validity.

PYTHIUM DACTYLIFERUM Drechsler, Proc. Cong. Internat. Soc. Sugarcane Tech. **3**: 122. 1930.

This species was enumerated together with others associated with root rot and seed piece decay of sugarcane in the United States by Rands. A later report by Rands and Dopp (1938b) state that this organism originally isolated in 1927 and thought to be an undescribed species and named *P. dactyliferum* by Drechsler has been subsequently identified by him as *P. irregulare*. Inasmuch as no description of the organism in question was presented the name becomes a *nomen nudum*.

PYTHIUM DAPHNIDARUM Petersen, Bot. Tidssk. **29**: 345–420. 1909.

This species is difficult to identify from the description given, particularly in the absence of information regarding the nature and origin of the antheridium. Petersen indicates that this species may be of doubtful status and that it may prove to be referable to *Pythium gracile* or *P. complens* upon further study. It is reported as parasitic on *Daphnia hyalina*, *D. cucullata* and *Bosmina coregoni* in Denmark.

PYTHIUM DICHOTOMUM Dangeard, Ann. Sci. Nat. VII. **4**: 313. 1886.

This species was imperfectly observed and described and probably is not a *Pythium*.

PYTHIUM FERAX de Bary, Bot. Zeit. **39**: 553–563. 1881.

Despite the description presented by de Bary, in the absence of figures and measurements it is difficult to ascertain the exact nature of the fungus with which he worked. *P. ferax* resembles *P. proliferum* and may be identical with it, though de Bary states that his fungus may be separated from *P. proliferum* on the basis of its possessing smaller hyphae, nonvacuolated sporangia and extramatrical oogonia. This fungus has not been observed since its original description.

PYTHIUM FIMBRIATUM de la Rue, Bull. Soc. Imp. Natur. Moscow **42**: 469. 1869.

This is a *nomen nudum*, inasmuch as no description of the fungus was presented.

PYTHIUM GIBBOSUM de Wildeman, Ann. Soc. Belg. Micros. **20**: 107–136. 1896.

De Wildeman described this fungus as a doubtful species of the genus, remarking that it resembled *Aphanomyces* very closely. No description is given as the fungus was not well understood; the species justifiably becomes a *nomen nudum*.

PYTHIUM GLOBOSUM Schenk, Verh. Phys.-Med. Gesell. Würzburg **9**: 12–31. 1859.

According to Matthews (1931) this species and one described by Schenk as *Pythium proliferum* are identical and both of them improperly assigned to this genus. According to Zopf (1890) and Butler (1907), these two fungi are probably *Myzoctium* and *Lagenidium*.

PYTHIUM GLOBOSUM Walz, Bot. Zeit. **28**: 553. 1870.

This fungus is presumably a mixture of *Pythium proliferum* of Schenk and *P. globosum* of the same author. Since these two organisms are thought to be *Myzoctium* and *Lagenidium*, Walz's fungus cannot be considered a member of the genus *Pythium*.

PYTHIUM HYDRODICTYORUM de Wildeman, Ann. Soc. Belg. Micros. **21**: 22. 1897.

This species is reported parasitic on *Hydrodictyon*. Since the description is incomplete and only the sexual stage was observed this species is of questionable validity.

PYTHIUM IMPERFECTUM Cornu, Ann. Sci. Nat. VI. **15**: 13. 1872.

The description given is not adequate to identify the species.

PYTHIUM INCERTUM Renny, Jour. Bot. **14**: 156. 1876.

Fischer (1892) does not consider this fungus to be a *Pythium* and Butler (1907) indicates that the identity of this species is very uncertain. Matthews (1931) concurs in this opinion.

PYTHIUM LATERALE Pringsheim, Jahrb. Wiss. Bot. **9**: 191–234. 1873–1874.

No detailed description of this fungus was given by Pringsheim, the fungus presented in an incidental manner when the author was comparing a few features in common with the imperfectly described *Pythium utriforme* of Cornu. *P. laterale* was said to differ from *P. utriforme* principally in the lateral orientation of the evacuation tube. The features presented are too meager to permit consideration of *P. laterale* as a valid species.

PYTHIUM MUSCAE Dangeard, Botaniste **22**: 325–490. 1931.

Only the asexual stage of this fungus was observed. Dangeard states that zoospores were formed in typical *Pythium* fashion. The following comment of Dangeard is worth mention: "Nous reconnaissons volontiers qu'une observation isolée n'a pas grande valeur: toutefois, comme le champignon en lui-même est intérressant, il nous a paru qu'on pouvait sans inconvenient le décrire sous le nom proposé plus haut." No host or locality are given.

PYTHIUM NICOTIANAE Van Hall, Med. Inst. Plantenzkt. **67**: 1–53. 1925.

This is a *nomen nudum*, no description of the fungus being given. It is possible that reference may have been intended to be for *Phytophthora nicotianae* Breda de Haan.

PYTHIUM PALMIVORUM Butler, Mem. Dept. Agric. India Bot. 1^5: 1–160. 1907.

Butler (1924) subsequently transferred this species to the genus *Phytophthora*.

PYTHIUM PLEROSPORON Sideris, Mycologia **24**: 14–61. 1932.

The description of this species is inadequate to identify it; in the writer's opinion it may prove to be synonymous with *Pythium rostratum*.

PYTHIUM POLYANDRUM Van Hall, Med. Inst. Plantenzkt. **67**: 1–53. 1925.

This is a *nomen nudum*, no description of the fungus being given.

PYTHIUM POLYSPORUM Sorokin, Trudy Obshch. Estestv. Imp. Kazan Univ. **2**: 23. 1872.

Butler (1907) excludes this species from the genus *Pythium* on the basis of its asexual and sexual stages; the writer concurs in this opinion. Matthews (1931) does not believe it to be a *Pythium*, but suggests that it may be a new genus of the Pythiaceae.

PYTHIUM PROLIFERUM Schenk, Verh. Phys.-Med. Gesell. Würzburg **9**: 12–31. 1859.

This fungus is not a *Pythium* species. It is thought to be a species of *Myzoctium* by Zopf (1890).

PYTHIUM SADEBECKIANUM Wittmack, Mitt. Ver. Ford. Moorkultur **10**: 83. 1892.

The inadequate description does not permit positive identification of the organism. It is possible that it may be a species of *Aphanomyces;* Jones and Drechsler (1925) and Matthews (1931) are of this opinion.

PYTHIUM TERATOSPORON Sideris, Mycologia **24**: 14–61. 1932.

Originally described as a *Pythium*, Sideris in a footnote transfers it to the genus *Phytophthora*. The writer considers this species to be identical with *Phytophthora drechsleri* Tucker; this observation has been confirmed by Tucker.

PYTHIUM TRACHEOPHILUM.

This name has been proposed for a pathogen causing stunt of lettuce. The fungus is treated in an unpublished thesis; consideration of it must await publication.

PYTHIUM UTRIFORME Cornu, Ann. Sci. Nat. VI. **15**: 13. 1872.

This fungus cannot be identified definitely from the description.

SUMMARY

A collection of over 2000 cultures of *Pythium* from various parts of the world and representing most of the known species was used in the investigation reported here.

The various isolates were grown on a number of different nutrient substrates for comparison of their growth habits and types of reproduction.

A detailed investigation of the morphology of the species indicated that the character of the sporangium, oogonium, antheridium and oospore could be used as criteria for the segregation of the species.

Isolates of all the species were grown on corn meal agar at temperatures ranging from 1° to 46° C. at 3° intervals. It was observed that different species varied considerably in their temperature relations. Different isolations of the same species behaved similarly indicating that the response to temperature is a specific feature. The temperature-growth relations are used as an adjunct to morphologic characters for identification of the species.

A description and discussion is given for each of the 66 species believed valid. Species reported and inadequately described or lacking description are listed as doubtful. Several species are shown to be synonymous with others, and the reasons for their elimination are included in the discussion of valid species. One new species, *Pythium hypogynum*, is presented.

A key based on certain morphologic features considered valid is provided for the identification of the species.

An attempt has been made to enumerate all the hosts on which the species are known to occur and their geographic distribution; this information is presented following the discussion of each species.

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GLOSSARY

acantha, spine.
acrogenous, originating or borne at the tip.
adnate, broadly and closely attached.
allantoid, sausage-shaped.
amphigynous, a basal type of antheridium which envelopes the oogonial stalk.
androgynous, antheridia and oogonia borne together or originating from the same hyphae.
apandrous, oospores formed in the absence of antheridia.
aplerotic, not filling.
appressorium, the flattened, thickened, or turflike tip of a hyphal branch by which the fungus is attached to the substrate.
arachnoid, resembling a spider's web.
catenulate, having a chainlike form.
clavate, club-shaped.
contiguous, an inflated portion in contact with another inflated portion, or near in succession through an intercommunicating filamentous portion.
dactyloid, finger-shaped.
diclinous, oogonia and antheridia arising from different hyphae, the antheridium not originating from the oogonial stalk.
digitate, finger-shaped.
diplanetism, the succession of two morphologically different phases of the swarm period always in the same sequence, separated by a rest period.
diverticulum, a pocket or closed branch opening off a main passage.
echinulate, spiny.
encystment, period of rest when a spore rounds-up and presents a visible wall.
endogenous, originating in the inside.
exogenous, originating on the outside.
falcate, sickle-shaped, hooked or curved like a sickle.
hyaline, colorless.
helicoid, spiral-shaped.
hypogynous, antheridium beneath the oogonium, specifically in the Pythiaceae either within the oogonial stalk or composed of a portion of the oogonial stalk adjacent to the oogonium.
inspissate, thickened.
intercalary, growth or development which is not apical but between the apex and the base.
monandrous, oospores formed in the presence of a single functional antheridium.
monoclinous, oogonia and antheridia arising from the same hyphae, the antheridium originating from the oogonial stalk.
monoplanetism, the condition of having one swarm phase, with no rest period.
moriform, mulberrylike culsters.
papilla, a nipple-shaped projection.
paragynous, the antheridium in lateral association with the oogonium, as opposed to *amphigynous*.
parthenogenesis, the process by which a new individual arises from haploid cells in the absence of fertilization.
plerotic, filling.
polyandrous, oospores formed in the presence of several functional antheridia.
pulvinate, cushion-shaped or strongly convexed.
refringent, refractive.
reticulate, netlike.
sigmoid, curved as in the letter *C* or doubly curved in different directions as in the letter *S*.
toruloid, resembling the genus *Torula*, chainlike; cylindrical portions with swollen intervening sections at varying intervals.

ADDITIONAL REFERENCES

There are a large number of references to hosts from which unidentified species of *Pythium* have been obtained. In the absence of any discussion of the fungus it is difficult to know just what disposition should be made of the

record. In order that the list of *Pythium* references may be made as complete as possible these entries are compiled and presented:

Agrostis sp. UNITED STATES: Nance (1940).
A. dispar Michx. ALSACE: Anonymous (1936b).
A. stolonifera L. ALSACE: Anonymous (1936b).
Albizzia sp. SUMATRA: Kuyper (1928).
Allium cepa L. UNITED STATES: Anderson (1924); Edson and Wood (1936); Newhall (1939).
Anacardium occidentale L. PALESTINE: Reichert (1939).
Ananas comosus Merr. HAWAII: Johnson (1935); Sideris and Paxton (1929).
Anona squamosa L. PALESTINE: Reichert (1939).
Antirrhinum majus L. UNITED STATES: Altstatt (1942); Nance (1940).
Apium graveolens L. var. *dulce* DC. BERMUDA: Whetzel (1922). CHINA: Yu (1940).
Arachis hypogea L. UNITED STATES: Edson and Wood (1937); Shaw (1936).
Avena sativa L. UNITED STATES: Edgerton, Tims and Mills (1929); Melhus (1938); Melhus, Reddy and Buchholtz (1939). CANADA: Robertson (1931).
Begonia tuberhybrida Voss. UNITED STATES: Nance (1939).
Beta vulgaris L. ENGLAND: Greeves and Muskett (1936). PALESTINE: Reichert (1939). UNITED STATES: Edson and Wood (1937); Kadow (1937); Nance (1939); Wood and Nance (1938).
B. vulgaris var. *macrorhiza*. BELGIUM: Roland (1938, 1939). CZECHOSLOVAKIA: Neuwirth (1934). DENMARK: Henning (1922). ENGLAND: Stirrup (1939). GERMANY: Greis (1940a, 1940b). NETHERLANDS: Brandenburg (1931a, 1931b, 1933, 1935); Van Poeteren (1933). UNITED STATES: Buchholtz (1935); Hutchison and Freeborn (1939); Leach (1941); Leach and Houston (1938); Lill (1930); Maxson (1938); Nance (1939, 1940); Wood and Nance (1938).
Brassica oleracea L. var. *botrytis* L. PALESTINE: Reichert (1939).
B. oleracea var. *capitata* L. UNITED STATES: Edson and Wood (1937); Martin (1933).
B. oleracea var. *italica* Plenck. PALESTINE: Reichert (1939).
B. pekinensis Rupr. PHILIPPINE ISLANDS: Fajardo (1934).
B. rapa L. UNITED STATES: Edson and Wood (1937).
Callistephus chinensis Nees. CZECHOSLOVAKIA: Smolak (1925).
Capsicum annuum L. CEYLON: Anonymous (1936a). PALESTINE: Reichert (1939). PUERTO RICO: Cook (1924). UNITED STATES: Edson and Wood (1937); Martin (1933); Nance (1939, 1940).
C. frutescens L. CHINA: Yu (1940).
Carica papaya L. CEYLON: Anonymous (1936a). HAWAII: Parris (1939b, 1941a). PALESTINE: Reichert (1939). TRINIDAD: Baker (1933).
Castanea sativa L. ITALY: Petri (1933).
Catalpa speciosa Warder. UNITED STATES: Wright (1937).
Chrysanthemum cocineum Willd. UNITED STATES: Sandsten (1934).
Cicer arietinum L. ARGENTINA: Fawcett (1941).
Citrullus vulgaris Schrad. UNITED STATES: Clinton (1934); Nance (1939, 1940); Newell (1941); Younkin (1938); Younkin and Melhus (1939); Walker (1939); Wood and Nance (1938).
Citrus sp. ARGENTINA: Blanchard (1930). UNITED STATES: Weindling (1932).
C. aurantifolia Swingle. BRAZIL: Muller (1933).
C. limonia Osbeck. BRAZIL: Muller (1933).
C. maxima Merr. TRINIDAD: Baker (1938).
Cocos nucifera L. JAMAICA: Ashby (1921). UNITED STATES: Weber (1923).
C. plumosa Hook. UNITED STATES: Weber (1923).
Colocasia esculenta Schott. HAWAII: Carpenter (1920); Parris (1936, 1938a, 1939a, 1940, 1941b).
Crassula portulacea Lam. UNITED STATES: Pirone (1937).
Cucumis melo L. var. *inodoratus* Naud. UNITED STATES: Nance (1940).
C. sativus L. ENGLAND: Salmon and Ware (1931). PALESTINE: Reichert (1939). UNITED STATES: Haenseler (1934); Haenseler and Allen (1934); Haenseler and Moyer (1937); Martin (1933); Nance (1940); Ramsey (1936, 1937); Wood and Nance (1938).

Cucurbita sp. UNITED STATES: Kadow (1937).
C. maxima Duchesne. PALESTINE: Reichert (1939).
C. pepo L. var. *condensa* Bailey. UNITED STATES: Edson and Wood (1936, 1937).
Curcuma longa L. CEYLON: Anonymous (1936a).
Cynodon dactylon Pers. UNITED STATES: Nance (1940).
Dalea sp. UNITED STATES: Buchholtz (1935).
Dendrobium sp. MAURITIUS: Wiehe (1941).
Euphorbia pulcherrima Willd. UNITED STATES: Brown (1940).
Fern prothallia UNITED STATES: Dodge (1940).
Festuca duriuscula L. ALSACE: Anonymous (1936b).
F. rubra L. ALSACE: Anonymous (1936b).
Foeniculum vulgare L. ITALY: Borzini (1937, 1938).
Fragaria chiloensis Duchesne. AUSTRALIA: Adam and Pescott (1932). CANADA: Berkeley (1936); Hildebrand (1934); Hildebrand and Koch (1936); Truscott (1934). ENGLAND: Alcock (1929); Berkeley and Lauder-Thompson (1934); Garret *et al.* (1939); Hickman (1940). FRANCE: Labrousse (1933). SCOTLAND: O'Brien and M'Naughton (1928); Wardlaw (1926). UNITED STATES: Bain and Demaree (1938); Brooks, Watson and Mowry (1929); Dowell (1931); Nance (1939); Plakidas (1930).
F. grandiflora Ehrh. PALESTINE: Reichert (1939).
F. vesca L. NETHERLANDS: Bouwens (1937).
Garcinia mangostana L. BURMA: Su (1933).
Gladiolus sp. UNITED STATES: Edson and Wood (1936, 1937).
Gossypium sp. ANGLO-EGYPTIAN SUDAN: Andrews and Clouston (1938); Clouston and Andrews (1940); Massey (1935, 1936). INDIA: Dastur (1931).
G. hirsutum L. UNITED STATES: Edson and Wood (1936); Lehman (1939); Miller (1938); Nance (1939); Weindling, Miller and Ullstrup (1941).
Hevea brasiliensis Muell. MALAYA: Beeley (1929, 1938); Sharples (1926, 1930, 1933); Thompson (1928); SUMATRA: De Jong (1941).
Hordeum vulgare L. CANADA: Robertson (1931). JAPAN: Asuyama (1935). TUNIS: Chabrolin (1927).
Ilex paraguensis St. Hill. ARGENTINA: Blanchard (1928).
Ipomoea batatas Lam. UGANDA: Hansford (1938). UNITED STATES: Brown (1940); Buchanan (1940); Harter (1924, 1925); Manns and Adams (1925); Wood and Nance (1938).
Juglans regia L. PALESTINE: Reichert (1939).
Lactuca sativa L. BERMUDA: Ogilvie (1926); Whetzel (1922). CANADA: Smieton and Brown (1940). PALESTINE: Reichert (1939). UNITED STATES: Clinton (1934); Nance (1940); Newhall (1939); Richards (1937); Wood and Nance (1938).
Lathyrus odoratus L. UNITED STATES: Martin (1933).
Lepidium sativum L. ENGLAND: Salmon and Ware (1938).
Lespedeza sp. UNITED STATES: Buchholtz (1935).
Leucaena glauca Benth. SUMATRA: Palm (1925); Palm and Jochems (1924).
Linum usitatissimum L. NETHERLANDS: Diddens (1932). UNITED STATES: Buchholtz (1935); Flor (1940); Nance (1939, 1940); Tervet (1937).
Lupinus sp. NORWAY: Solberg (1926).
Lycopersicon esculentum Mill. AUSTRALIA: Samuel (1930). CHINA: Yu (1940). ENGLAND: Salmon and Ware (1931). HAWAII: Parris (1938b). JAMAICA: Hansford (1924). PALESTINE: Reichert (1939); Altstatt (1942); Beach and Shuk (1941). UNITED STATES: Harrison, Young and Altstatt (1939); Martin (1933); Nance (1939, 1940); Skinner (1939).
Mangifera indica L. PHILIPPINE ISLANDS: Camus (1935).
Medicago sativa L. UNITED STATES: Buchholtz (1934, 1935); Edson and Wood (1936, 1937); Grandfield, Lefebvre and Metzger (1935).
Melilotus alba L. UNITED STATES: Buchholtz (1935); Heald (1931); Humphrey and Wood (1935).
M. indica L. UNITED STATES: Buchholtz (1935).
Musa textilis Nee. PHILIPPINE ISLANDS: Hernandez (1924); Roldan (1933).
Nicotiana tabacum L. ALSACE: Anonymous (1936b). CANADA: Berkeley (1937); Hildebrand and Koch (1936); Koch (1935, 1937). CEYLON: Anonymous (1936a); Park (1937); Park and Fernando (1937); Paul and Fernando (1938). JAVA: Leefmans (1934). PUERTO RICO: Cook (1925). RUSSIA: Grooshevoy and Levykh (1936). SUMATRA: Jochems (1926,

1927a, b, 1933a, b); Meurs (1931); Sidenius (1922); Van der Goot (1928, 1934, 1935, 1937); Van Hall (1924, 1926). UGANDA: Hansford (1938). UNION SOUTH AFRICA: Doidge and Bottomley (1931); Moore (1926); Moore and Smith (1936). UNITED STATES: Anderson, Swanback and Street (1938); Cooper (1929); Edson and Wood (1936); Johnson (1937, 1939); Nance (1939, 1940); Valleau and Johnson (1939); Wood and Nance (1938).

Oryza sativa L. JAVA: Leefmans (1929, 1930). UNITED STATES: Cralley and Tullis (1937); Edson and Wood (1937); Gray (1934); Ryker (1937).

Panicum barbinode Trin. HAWAII: Martin (1937).

Pelargonium sp. CEYLON: Anonymous (1936a); Haigh (1929). ITALY: Petri (1935). UNITED STATES: Gill (1936); Holdridge and McCubbin (1928).

P. zonale L'Her. UNITED STATES: White (1938).

Persea americana Mill. PHILIPPINE ISLANDS: Roldan (1933).

Phaseolus lunatus L. UNITED STATES: Martin (1933).

P. vulgaris L. CHINA: Yu (1940). NORWAY: Solberg (1926). PALESTINE: Reichert (1939). PHILIPPINE ISLANDS: Fajardo (1934). SIERRA LEONE: Deighton (1936). UNITED STATES: Edson and Wood (1936); Wood and Nance (1938).

Phoenix dactylifera L. PALESTINE: Reichert (1939).

Physalis peruviana L. PALESTINE: Reichert (1939).

Phytolacca octandra L. SUMATRA: Palm (1925); Palm and Jochems (1924).

Pinus sp. UNITED STATES: Edson and Wood (1936); Nance (1939, 1940).

P. banksiana Lamb. UNITED STATES: Hansen *et al.* (1923); Stakman (1923).

P. insignis Dougl. INDIA: C (1927).

P. insularis Endl. PHILIPPINE ISLANDS: Roldan (1933).

P. longifolia Roxb. INDIA: C (1927).

P. massoniana Lamb. PHILIPPINE ISLANDS: Roldan (1933).

P. pinea L. ITALY: Petri (1940).

P. ponderosa Dougl. UNITED STATES: Jackson (1933).

P. resinosa Ait. UNITED STATES: Hansen *et al.* (1923); Stakman (1923); Wiant (1929).

P. strobus L. UNITED STATES: Hansen *et al.* (1923); Stakman (1923).

Pisum arvense L. NETHERLANDS: Brandenburg (1931a, 1931b).

P. sativum L. CANADA: Anonymous (1924a). ENGLAND: Baylis (1941); Croxall and Ogilvie (1940). NETHERLANDS: Brandenburg (1935). NEW ZEALAND: Hyde (1939). NORWAY: Solberg (1926). UNITED STATES: Drechsler (1925); Edson and Wood (1936, 1937); Haenseler (1924); Horsfall and Kertesz (1933); Jones (1925); Jones and Linford (1925); Kadow (1937); Martin (1933); Nance (1940); Sharvelle and Shema (1941); Wood and Nance (1938).

Poa compressa L. ALSACE: Anonymous (1936b).

P. pratensis L. ALSACE: Anonymous (1936b).

Pogostemon cablin Benth. UGANDA: Hansford (1938).

Prunus amygdalus L. PALESTINE: Reichert (1939).

Pseudotsuga taxifolia Britt. UNITED STATES: Jackson (1933).

Pyrus communis L. CZECHOSLOVAKIA: Baudys (1930).

Raphanus sativus L. UNITED STATES: Edson and Wood (1936, 1937).

Ricinus communis L. HAWAII: Weiss (1942).

Robinia pseudo-acacia L. UNITED STATES: Weiss (1942); Wright (1937).

Rubus idaeus L. CANADA: Berkeley (1936).

Saccharum officinarum L. AUSTRALIA: Bell (1929). EGYPT: Rosenfeld (1939). HAITI: Ciferri (1928). HAWAII: Agee (1926); Barnum (1927); Barnum and Zwaluwenburg (1927); Carpenter (1919, 1921, 1928c, 1934); Cooke (1933); Lee (1928); Lee, Barnum, Weller and Carpenter (1927); Lyon (1923); Martin (1937). INDIA: Ramakrishna (1941); Subramaniam (1936b). MAURITIUS: Hill (1931); Shepherd (1925, 1931, 1933); Wiehe (1940a, b). PHILIPPINE ISLANDS: Agati (1931); Ocfemia (1931); Roldan (1930). PUERTO RICO: Bourne (1924); Cook (1930); Earle (1920); Matz (1920, 1921). SUMATRA: Kuyper (1930); Treub (1885). UNION SOUTH AFRICA: McMartin (1937). UNITED STATES: Dowell (1931); Edgerton and Moreland (1921); Edgerton, Taggart and Tims

(1924); Edgerton and Tims (1925, 1927); Edgerton, Tims and Mills (1929); Flor (1930a, 1930b); LeBeau (1939); Lee, Weller and Barnum (1926); Nance (1939, 1940); Stevenson and Rands (1938); Tims (1932a); Tims and Mills (1927).

Secale cereale L. CANADA: Robertson (1931).

Senecio cruentus DC. UNITED STATES: Drechsler (1935).

Sinningia speciosa Benth. and Hook. GERMANY: Landgraf (1932).

Soil. UNITED STATES: Harvey (1927, 1929); Jensen (1912); Raper (1928).

Solanum melongena L. PALESTINE: Reichert (1939). UNITED STATES: Martin (1933).

S. tuberosum L. PALESTINE: Reichert (1939). UNITED STATES: Ramsey (1937); Ramsey and Wiant (1938); Shapovalov and Link (1924).

Sorghum vulgare Pers. UNITED STATES: Edson and Wood (1937); Hoffmaster (1942); Hutchison and Freeborn (1939); Nance (1940).

S. vulgare var. *sudanense* (Piper) Hitchc. HAWAII: Martin (1937). UNITED STATES: Lefebvre and Johnson (1941).

Soya max L. UNITED STATES: Kent (1942).

Spinacea oleracea L. UNITED STATES: Cook and Callenbach (1935); Edson and Wood (1936, 1937); Kadow (1937); Martin (1933); Wood and Nance (1938).

Stevia sp. UNITED STATES: Brown (1940).

Thea sinensis L. INDO-CHINA: Pfältzer (1940). MAURITIUS: Shepherd (1933).

Trifolium sp. NORWAY: Solberg (1926).

T. hybridum L. UNITED STATES: Buchholtz (1935).

T. pratense L. UNITED STATES: Buchholtz (1935).

T. repens L. UNITED STATES: Buchholtz (1935).

Triticum aestivum L. CANADA: Robertson (1931); Simmonds (1939a, b); Simmonds, Russell and Sallans (1935); Vanterpool (1935a, c); Vanterpool and Ledingham (1930). ITALY: Biraghi (1936); Paolis (1931); Petri (1930, 1936). JAPAN: Asuyama (1935). UNITED STATES: Brown (1940); Edgerton, Tims and Mills (1929); Maneval (1937); Nance (1940); Wood and Nance (1938).

Tulipa gesneriana L. ENGLAND: Moore (1940a); Moore and Buddin (1937).

Ulmus americana L. UNITED STATES: Wright (1937).

U. pumila L. UNITED STATES: Wright (1937).

Vicia faba L. NETHERLANDS: Brandenburg (1931a, 1935).

Vigna sinensis Endl. UNITED STATES: Wood and Nance (1938).

Viola tricolor L. ENGLAND: Chesters and Hickman (1939). NETHERLANDS: Van Eek (1938).

Washingtonia robusta Parish. UNITED STATES: Weber (1923).

Wood pulp. ITALY: Goidanich (1938).

Zea mays L. INDIA: Padwick (1940); PHILIPPINE ISLANDS: Agati (1931); Roldan (1930); UNITED STATES: Cooper (1927, 1929); Edson and Wood (1936). LeBeau (1939); Nance (1939, 1940); Robbins (1927); Valleau, Karraker and Johnson (1926); Wood and Nance (1938).

Zingiber officinale Roscoe. CEYLON: Anonymous (1936a). HAWAII: Parris (1939b, 1940). INDIA: Thomas (1939, 1941).

Pythium spp. have been reported from the United States on unspecified hosts such as conifers (Wilde, 1937), flower and vegetable seedlings (Linn, 1937) and herbaceous and woody plants (Osmun, 1934).

Some reports fail to distinguish between damage due to *Pythium* sp. and *Rhizoctonia* sp., listing hosts for both fungi. It is difficult to determine in some cases whether *Pythium* spp. participated at all in the reduction and loss of stand. These lists are often extensive, including ornamentals as well as fruit and vegetable crops. The reader is referred to Adams (1935), Anderson, Kadow and Hopperstead (1937), Doran (1928, 1938), Dunlap (1936a, 1936b) and Kadow and Anderson (1937).

There are a few reports which cite hosts as attacked by either *Pythium* or *Phytophthora* and in some instance by a "Pythium-like" organism. Hosts

listed for such fungus reports are: *Dioscorea batatas* Decne., Jamaica (Hansford, 1923), *Eugenia aromatica* Baill., Madagascar (Heim and Bouriquet, 1937), *Grammatophyllum speciosum* Blume, Seychelles (Squibbs, 1938), *Hibiscus sabdariffa* L., Ceylon (Gadd, 1936) and *Musa* sp., Italian Somaliland (Petri, 1932).

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